THE APICAL DEVELOPMENT, AND THE EFFECTS OF CHLORMEQUAT AND ETHEPHON ON THE DEVELOPMENT, PHYSIOLOGY AND YIELD OF SPRING BARLEY

by

Baoluo Ma

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Department of Plant Science
Macdonald College of
McGill University
Montreal, Quebec
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Short title

EFFECTS OF CHLORMEQUAT AND ETHEPHON ON BARLEY PHYSIOLOGY

Baoluo Ma

ABSTRACT

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THE APICAL DEVELOPMENT, AND THE EFFECTS OF CHLORMEQUAT AND ETHEPHON ON THE DEVELOPMENT, PHYSIOLOGY AND YIELD OF SPRING BARLEY

Plant growth regulator(s) (PGR) can be used as lodging inhibitors and/or yield promoters for spring barley (Hordeum vulgare L.) From 1987 to 1990 four field experiments were conducted to monitor barley main-stem apical development and to determine the effects of chlormequat (CCC) and ethephon on the development, physiology and yield of spring barley Our data provide a description of barley apical development and the general pattern of leaf and spikelet primordium production under field conditions In general, PGR treatment reduced the apical dominance of dominant sinks allowing the survival and greater development of more subordinate sinks. Early application of either CCC or ethephon retarded development of the main-stem apex from shortly after application to the awn elongation stage and reduced the number of aborted spikelet primordia, thus increasing the potential number of grains per spike and sometimes grain yield. Ethephon applied at ZGS 39 reduced plant height and lodging. Early application (ZGS 30) of ethephon, alone or in combination with CCC increased the number of spikes m^{-2}, but not grain yield. The number of spike-bearing shoots per unit area or per plant was increased by early PGR treatment, primarily by enhancement of tiller number rather than tiller survival. Early application of CCC or ethephon to spring barley is not justified, and caution must be taken when using ethephon at the currently recommended rate and stage for lodging control. Post-anthesis application of ethephon can efficiently enhance grain fill and yield of spring barley.

RESUME

DÉVELOPPEMENT APICAL, ET LES EFFETS DU CHLORMEQUAT ET DE L'ETHEPHON SUR LE DÉVELOPPEMENT, LA PHYSIOLOGIE ET LE RENDEMENT DE L'ORGE DE PRINTEMPS

Les régulateurs de croissance (RC) peuvent être utilisés comme inhibiteurs de la verse et/ou promoteurs du rendement de l'orge de printemps (Hordeum vulgare L.). De 1987 a 1990, 4 expériences ont été conduites dans le champs pour suivre le développement apical de la tige principale et pour determiner les effets du chlormequat (CCC) et l'ethephon sur le développement, la physiologie et le rendement de l'orge de printemps. Nos résultats décrivent le développement apical de l'orge et le modèle général de la production des primordia foliaires et des épillets dans les conditions champêtres. En général, les régulateurs de croissance (RC) réduisent la dominance apicale des cibles dominantes permettant aussi la survie et un meilleur développement des cibles subordonnées. Une application hâtive de CCC ou de l'ethephon a retardé le développement apical des tiges principales jusqu'au stade de l'élongation des barbes, et a réduit le nombre des primordia avortés des épillets, élevant aussi le nombre de graines par épi et parfois le rendement en graines. Ethephon, appliqué au ZGS 39 a réduit la taille et la verse des plantes. Une application hâtive de l'ethephon seul ou en combinaison avec le CCC a élevé le nombre d'épis par m^2, mais pas le rendement en graines Le nombre des tiges portant des épis par unité de surface et par plante a été élevé par un traitement aux RC, en élevant le nombre des thalles plutôt que leur survie. Une application hâtive de l'ethephon et du CCC a l'orge de printemps n'est pas justifiée, et on devrait être prudent en utilisant l'ethephon à la concentration et au stade recommandés pour le contrôle de la verse. Une application de l'ethephon après la floraison peut accroitre efficacement le remplissage des graines et le rendement de l'orge de printemps.

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CONTRIBUTIONS OF CO-AUTHORS TO MANUSCRIPTS FOR PUBLICATION

The contents of sections 3 to 9 (inclusive) are drawn, respectively, from the manuscripts for publication, Ma and Smith (1991a, 1991b, 1991c, 1991d, 1991e, 1991f, 1991g). These seven manuscripts were co-authored by myself and my supervisor, Dr. D.L. Smith. Dr. Smith provided funds, assistance and normal supervisory guidance from the outset of the research to the reviewing of the manuscripts before submission for publication.

Section 1

INTRODUCTION

Barley (Hordeum vulgare L.) is one of the world's major food and feed grain cereal crops. This is because of its adaptation to a wide spectrum of climate and soil-fertility regimes. The world production of barley has increased by more than 60 % in the past two decades, mainly due to progress in breeding and managerial husbandry practices. Breeding barley for higher yield and better quality, like other cereal crop breeding, seems to be at a plateau. Continued progress may be possible through a better understanding of the development and functioning of the barley plant.

The grain yield of barley is usually divided into several components: the number of spikes per plant or per unit area, the number of grains per spike and the mean grain weight (Petr et al., 1988; Gebeyehou et al., 1982). These components are closely related to apical development and processes of grain fill. Apical development determines the number of spike-bearing shoots as well as the number of grains per spike, and grain fill determines the grain size and plumpness through partitioning of photoassimilates among plant organs.

Since the discovery of chlormequat (2-chloroethyl trimethylammonium chloride, chlorocholine chloride, CCC, commercially known as Cycocel) as an anti-lodging agent for wheat crops in the early 1960's (Cyanamid, 1966), the use of plant growth regulator(s) (PGR) on cereal crops has offered a new and potentially powerful cultural practice for the managerial control of plant growth and

development, leading to increased yield (Koranteng and Matthews, 1982; Wareing, 1976).

That PGR application to cereal crops results in shortening of stems and subsequent control of lodging has been clearly demonstrated (Paterson et al., 1983; Dahnous, 1982). However, yield increases following CCC or ethephon (2-chloroethyl phosphonic acid, commercially known as Cerone, Ethrel or Camposan) treatment are not consistent (Paterson et al., 1983). This has restricted the large-scale use of these PGR (Leary and Oplinger, 1983). Moreover, yield reductions due to these PGR have been reported for spring barley, winter barley (Paterson et al., 1983), and corn (Zea mays L.) (Gaska and Oplinger, 1988a). For example, in Scotland, a 4 year regional test with spring and winter barley cultivars (Paterson et al., 1983) showed that ethephon was generally ineffective, with only 11 % of the treatments resulting in an economic increase in grain yield. Chlormequat or Terpal C (a 2:1 mixture of chlormequat and ethephon) resulted in an economic increase in grain yield in only 36 % and 20 % of treatments, respectively. Furthermore, a statistically significant yield reduction due to chlormequat or ethephon was found in 16 % and 17 % of treatments, respectively. Brown and Earley (1973) showed that application of ethephon to oat resulted in a grain yield reduction. Green et al. (1988) reported that mepiquat chloride (1,1 - dimethyl - piperidinium chloride), which produces effects similar to chlormequat, had the potential to increase grain yield only under conditions of lodging. The causes of the widely varying responses to PGR treatment are uncertain, and the physiological bases of PGR action are not fully

understood.

1.1 Hypotheses

For the work described herein it was hypothesized that:

(1) under north eastern North American continental climatic field conditions apical development and primordium production of spring barley will have a distinguishable sequence of developmental characteristics, similar to those previously reported either under controlled environment or European field conditions but with a time sequence unique to the locale;

(2) early application of CCC or ethephon at Zadoks (Zadoks et al., 1974) growth stage (ZGS) 13 or ZGS 30 will reduce the rate and speed of the mainstem apical development, since CCC functions as an anti-gibberellin agent (Jung, 1984); and ethephon affects auxin biosynthesis and transport (Woodward and Marshall, 1988);

(3) suppression of apical dominance of the main stem will encourage tiller growth and survival, resulting in more synchronous development of barley shoots within a plant and/or within a spike, resulting in more ear-bearing tillers and/or a greater number of grains per spike;

(4) this effect will alter the relationship between the stages of the apical development and the vegetative stages;

(5) early application of ethephon alone or in combination with CCC to spring barley will increase the number of spike-bearing shoots and/or grain yield;

(6) late application of ethephon (1-wk after heading) will alter

the grain mass without substantial effects on other yield components, resulting in an increase in grain yield.

Objectives

In this study, four field experiments were carried out for 4 years, from 1987 to 1990, at the Emile A. Lods Agronomy Research Center, Macdonald College of McGill University. The overall objectives were:

(i) to monitor the apical development of spring barley cv. 'Cadette' and 'Leger' from the vegetative apex stage to spike formation;

(ii) to evaluate the effects of CCC and ethephon on apical development;

(iii) to test the effect of CCC and ethephon application timing on barley tillering patterns and dynamics;

(iv) to determine the effects of the time of CCC or ethephon application on yield components and grain yield;

(v) to ascertain the effect of early ethephon alone, or in combination with CCC application (ZGS 30, the beginning of mainstem elongation) on the production of spike-bearing shoots and their contribution to grain yield;

(vi) to evaluate the effect of late ethephon application (ZGS 65, 1-wk after heading) on dry matter allocation to the grain and the overall yield response;

(vii) to develop a system for studying the mechanism of N assimilation and redistribution and possibly other growth effectors such as PGR on spike dry matter allocation and N deposition.

Section 2

LITERATURE REVIEW

2.1 Importance and Use of Barley Crops

Barley (Hordeum vulgare L.) is one of the oldest cereal crops and one of the major contemporary feed and food grains. Barley production has spread to many regions of the world from its probable origin in the Fertile Crescent of the Near East, and it is now grown in more diverse climates and on more varied soil types than any other cereal. It is also found on the agricultural margins, such the high plateaus of Tibet of China and Ethiopia, or the Andes Mountains of Peru. It is produced on the fringes of the Sahara and north of the Arctic Circle, farther north than any other cereal (Poehlman, 1987). Barley is the world's fourth most important cereal crop, after wheat (Triticum aestivum L.), corn (Zea Mays L.), and rice (Oriza sativa L.), the fourth ranking cereal in the USA and the second ranking cereal in Canada. It is the most widely grown small grain cereal in Quebec, covering 160,000 ha.

World population has already passed five billion and is still increasing at a speed of about ninety million per year. World food production, thus far, has kept pace with the growth in population. However, with ever increasing world population, rapid progress in both plant breeding programs and managerial strategies is vital. Barley has a role to play in this increased world grain production.

Barley is the basis of the malting industry (Peterson and Foster,

1973) and the predominant feed grain in Canada, and in those area of the USA where corn and sorghum are not adapted (Baldridge et al., 1985). In North America, barley has two principal commercial uses. One is for feed or livestock and the other is for malting (Wilson, 1985). The largest domestic use of barley, accounting for about 50 %, is as a feed crop for livestock in the USA (Metcalfe and Elkins, 1980). About 30 % of the barley grain is used for malting. Malt is used in the production of beer, distilled alcoholic products, malt syrup, breakfast foods and coffee substitutes. The portion used for human food is small (Foster and Prentice, 1987). Barley food products are mainly pot and pearled barley, barley flours, and barley grits. In some areas of the USA, particularly the West, a considerable acreage of barley is utilized for pasture or hay. It is often used as a companion crop for alfalfa in irrigated regions of the West.

A distinguishing feature of barley grain production in Canada is the few types (Malt or feed) of grain which are produced, relative to those in the USA (Wilson, 1985). Barley production in the three prairie provinces accounts for about 90 % of the Canadian total. More than 80 % of barley grain is used for malting in both Saskatchewan and Alberta, and slightly less than half grain produced in Manitoba is used for feed. Since 1974 the area planted to malting cultivars has increased substantially (Wilson, 1985). In Quebec, barley is mainly grown for feed. Data on total supply and demand for barley in Canada indicate that the quantity of barley used for feed has increased steadily since 1967, while the amount of barley used for malting has increased only slightly during the same period. Exports of barley

have also increased remarkably. In general, the major use of Canadian barley is for domestic livestock feed and for export. Malt barley accounts for only about 10 percent of total domestic use (Wilson, 1985).

2.2 Structure of Barley Spike

The developmental processes of the barley inflorescence are in fact the sequential formation of each component. After a number of leaves have been initiated, the shoot apex differentiates to give rise to spikelet initials. At first, the apex lengthens, then double ridges develop to initiate the formation of each reproductive organ. Therefore, examining the structure of the spike is essential to understanding the whole course of the young-ear development.

The inflorescence of a barley plant is a spike (or an ear) located at the tip of the culm. The axis of the spike, the rachis, is usually bilateral symmetrical. The basal node of the rachis is a 'collar'. Typically, three spikelets arise at each node of the rachis, and these triplets alternate from side to side throughout its length. Each spikelet normally consists of one floret and two narrow glumes. This single-floret spikelet distinguishes the barley inflorescence from wheat. A floret is composed of a lemma, a palea, a carpel and three stamens. At maturity, the lemma and palea remain attached to the caryopsis after threshing in most barley cultivars, and thereby the barley caryopsis is often called a 'seed' or a 'grain', but not a kernel (Dr. H. R. Klinck, 1988, personal communication), and is referred to coarse grain. The central spikelet

at each node is the largest with laterals ranging from fully fertile to completely sterile, thereby forming six-rowed or two-rowed barleys (Stoskopf, 1985; Reid and Wiebe, 1979). In six-rowed cultivars all three spikelets are fertile, while only the central one is fertile in two-rowed barleys. It has been reported that six-rowed barley is derived from a two-rowed ancestor. The six row phenotype is controlled by one pair of recessive genes (Harlan, 1975).

2.3 Barley Inflorescence Differentiation

An understanding of the development of cereal crop inflorescences is of fundamental importance. During the pre-heading phase aspects of inflorescence development as well as spike growth greatly influence the production and survival of florets (spikelets in barley) and thus grain number (Waddingdon et al., 1983). The processes of shoot apex differentiation have been much investigated by many workers (Frank and Apel, 1985; Knopp, 1985; Baker and Gallagher, 1983; Waddington et al., 1983; Appleyard et al., 1982; Kirby and Appleyard, 1981; Hejnowicz and Wloch, 1980; Kirby and Riggs, 1978; Kirby, 1977; Kirby, 1974; Langer and Hanif, 1973; Bonnett, 1966; Nicholls and May, 1963; Bonnett, 1935). Detailed descriptions of each apex developmental stage of barley are summarized in Table 2.1. Many other workers have also designed scales to describe apical development and morphogenesis. For example, Aspinall and Paleg (1963) adopted 11 stages to describe the processes of barley apical development. A similar, but more detailed description with fewer stages was reported by Kirby and Faris (1970).

Waddington et al. (1983) listed and compared various scales describing the apical development and morphogenesis of barley and wheat.

Table 2.1 Scales and description of barley apical development

Stage No.	Description
1	Vegetative stage (apex not elongating). The apex differentiates leaf and stem node initials.
2	Transition stage (apex elongating). This marks the end of the vegetative apex, and the differentiation of leaf primordia and internode initials is finished.
3	Double ridge stage. It is the first indication of spike differentiation and spikelet primordia can be recognized. The double ridges refer to spikelet initials generated from the axils of modified leaf primordia which forms the lower ridge, i.e. a leaf primordium ridge and a spikelet primordium ridge stacked together form a double structure.
4	Upper ridge enlarging. It is a period of the rapid development of spikelet initials with the leaf primordia suppressed.
5	Triple mound stage. Lateral spikelets are visible as three distinct mounds. The median mound is the primordium of the median spikelet, and the two flanking mounds will give rise to the lateral spikelets
6	Glume primordium stage. Glumes are the first structures

Table 2.1 Cont'd

of the spikelet to differentiate. This stage lasts only a short time.

7 ..... Lemma primordium stage. Strictly speaking, the appearance of lemma initial is the real start of floret differentiation.

8 ..... Stamen primordium stage. Three papillae (stamen primordia) appear on the meristem above the lemma.

9 ..... Awn primordium stage. An outgrowth from the lemma forms the awn primordium. This marks the completion of spikelet initiation phase, and the number of primordia reaches a maximum value.

10 ..... Awn longer than spikelets. This is a long period during which megasporogenesis and microsporogenesis take place.

11 ..... Anthesis. The formation of pollen and embryo sac and subsequent pollination marks the end of apical development and the beginning of grain filling phase.

Adapted from Aspinall and Paleg' (1963) scale and modified with Kirby and Appleyard' (1981) description.

2.4 Factors Affecting the Apical Development

Environmental factors which affect the shoot apical development in cereal crops have been extensively studied. These factors include temperature (Baker and Gallagher, 1983; Rahman and Wilson, 1978; Warrington et al., 1977; Halse and Weir, 1974; Purvis, 1934), light (Baker and Gallagher, 1983; Kirby and Appleyard, 1980; Rahman et al., 1977; Aspinall and Paleg, 1963), day length (Kirby and Appleyard, 1980; Allison and Daynard, 1976), and day length and temperature interaction (Barham and Rasmusson, 1981; Tew and Rasmusson, 1978). Attention has also been given to some field managerial factors such as plant population (Kirby and Faris, 1970), water stress (Nicholls and May, 1963), sowing date (Wright and Hughes, 1987; Kirby et al., 1985) and use of plant growth regulators (Petr et al., 1988; Hofner and Kühn, 1982; Williams and Cartwright, 1980).

In a morphogenetic study, Kirby and Faris (1970) in Great Britain, focused on the spike development of the main culm of the two-rowed barley cv. Proctor, grown at densities ranging from 50 to 1600 plants m^{-2}. They found that leaf number, leaf size, stem and internode length, apex development and primordia production were all noticeably affected by plant density. For example, the number of fully expanded leaves was decreased from 10.2 in the lowest density treatment to 8.0 with 1600 plant m^{-2}. This led to earlier floral initiation in the highest density treatment and the plants of the high density populations reached the double ridge stage six days earlier than those at low densities. The rate of spikelet primordium formation was not significantly affected by plant density, but spikelet primordium

abortion occurred earlier, and spikelet survival was much lower in the high density treatment. Kirby and Faris argued that the sudden cessation of primordium production at the high density, which resulted in shorter ears, was probably attributable to morphological differences of the apex and a high concentration of gibberellins in the tissue. The high levels of gibberellins promoted earlier competition for nutrients. The competition resulted from the poorly developed vascular tissue, leading to starvation and death of the apex tip (Kirby and Faris, 1970).

Studying the relationships among primordium formation, apex length, and spikelet development in Australia, Nicholls and May (1963) reported that although the duration of spike initiation is somewhat longer under water-stressed conditions, during the spike initiation period, the total number of spikelet primordia was reduced as the spikelets were initiated at a lower rate.

Change of sowing date, which effectively changes the temperature, and the photoperiod, has a large effect on the apical development of cereal crops. Wright and Hughes (1987) investigated the effects of 13 sowing dates on the leaf appearance, spikelet initiation and mainstem apical development in spring barley cv. 'Triumph' over four years. They found that delaying sowing was associated with faster rates and shorter durations of leaf appearance and spikelet initiation, and shorter time to attainment of all stages of the apical development.

Recently, intensive cereal management practices have been used with some success in Europe, and trials in North America have indicated that a significant yield benefit may be derived from their

use under certain climatic conditions (Mohamed et al., 1990; Fredrick and Marshall, 1985). The management practices involve the use of responsive high yielding cultivars grown with high levels of N fertilization, in narrower row spacings than are conventionally used and with the application of growth regulators and pesticides (herbicides and fungicides in particular). High N fertility accompanied with high plant densities and narrower rows promote lodging and pest development in cereals, but proper use of PGR and pesticides may aid in maintaining the high yield potential generated by high inputs.

Hormone-based herbicides may induce inflorescence abnormalities in cereals when applied at the apex sensitive stage (Thomson et al., 1984), while application of PGR to promoter tiller production or other alterations may not function well when applied at non-optimal apex stages (Cartwright and Jaddoa (1985). There has been considerable interest in the hormonal manipulation of growth and developmental relationships between the main-stem and tiller shoots and/or within the spike (Petr et al., 1988; Höfner and Kühn, 1982; Hutley-Bull and Schwabe, 1982; Williams and Cartwright, 1980).

Williams and Cartwright (1980), in Great Britain, examined the effects of a cytokinin, 6-benzyl-amino purine (BAP), in a pot experiment on the gradients of shoot and spikelet size within the plant during the pre-heading period, and their relation to final grain yield. They found that grain yield per plant was increased 57 % by the application of BAP at ZGS 13, although it was unaffected by the "late" (ZGS 30) BAP treatments. The greater production of grains was mainly

due to tillers and to the basal distal parts of the spike. Therefore, they concluded that application of the cytokinin can increase uniformity both among shoots within a plant (main spike and tiller spikes) and among spikelets within the ear.

Petr et al. (1988) working in Czechoslovakia, recently reported that early application of CCC (locally known as Retaced) to winter cereals during Feekes growth stage 3 to 7 (Large, 1954), equivalent to ZGS 15 to 32, delayed the differentiation of the apex by 1 to 1.5 stages, which resulted in increased tillering and a greater number of ears per unit area. Similar results with spring barley treated with CCC and Terpal were also mentioned in their paper.

Hutley-Bull and Schwabe (1982) stated that the responses engendered by early GA_3 treatments are very similar to those produced by intercalating periods of longer days in a standard photoperiodic regime, while the effects of CCC and other retardants resemble those brought about by the intercalation of shorter days. Thus, gibberellin treatment tends to hasten development, advances spikelet differentiation and reduces leaf, spikelet and tiller numbers, whereas retardants such as CCC and Paclobutrazol ([2RS, 3RS]-1-[4-chlorophenyl]-4,4-dimethyl-2-[1,2,4-triazol-1-yl]pentan-3-ol; PP333) have the opposite effect.

In Great Britain, Cartwright and Jaddoa (1985) sprayed CCC at 1.15 kg ha^{-1} in winter barley (at a density of 250 plants m^{-2}) at the lemma primordium stage. They found that the treatment transiently retarded development and elongation of the more advanced shoots and lessened their dominance so that growth and survival of higher order

tillers was promoted; and commented that in barley the retarding effect of early CCC is transient but the associated increase in 'sink size' is persistent.

Thomson et al. (1984) working in Northern Scotland, found that hormone-based herbicides ((Mecoprop, MCPA, Mecoprop/bromoxynil/ioxynil mixture) applied to winter barley after the triple mound apex stage produced few or no abnormalities while such abnormalities were evident when the herbicides were applied earlier in development, at the late vegetative and double ridge stages when the apex is changing from leaf to spikelet primordium production.

2.5 Tillering and Tiller Contribution to Grain Yield

2.5.1 Tillering and Tiller Dynamics

Tillers are the lateral shoots of cereal crops and other grasses. The anatomy and growth of tillers has been reviewed by several authors (Williams and Langer, 1975; Williams et al., 1975; Fletcher and Dale, 1974), so that only a brief summary will be presented. Tillers arise from small axillary buds within a cavity in the axil of leaves (or leaf-like structures such as the coleoptile and prophyll, a coleoptile analogue preceding the first true leaf on a tiller) and stems. As these buds grow, they break out of their cavity and elongate between the leaf sheath and the stem until they emerge. Tillers remain fully dependent on their parent shoot, specifically on the leaf located immediately above the subtending leaf (Fletcher and Dale, 1974), until they have established a sufficient number of leaves (generally 3) and roots to satisfy their own needs for photosynthates and nutrients.

Tillers produced in the axil of main stem leaves are referred to as primary tillers. These, in turn, produce secondary tillers, which bear tertiary tillers, and so on. Secondary, tertiary, and their respective tillers are often called 'higher-order tillers'.

Every tiller has the potential of producing an inflorescence, yet, only a relatively small proportion of the tillers produced will survive to maturity and produce grain. Factors which influence the production and survival of tillers can ultimately influence yield via effects on final ear numbers. Cereals generally produce tillers in a definite and fairly consistent pattern (Klepper et al., 1983; Masle-Meynard and Sebillotte, 1981b; Rawson, 1971) which closely follows leaf appearance (Kirby et al., 1985; Baker and Gallagher, 1983; Friend, 1965). Environmental stresses can restrict the growth of tiller buds so that they never emerge (Williams et al., 1975; Aspinall, 1961).

Tiller numbers per plant or per unit area in the field rise to a peak and then decline more or less rapidly (Hucl and Baker, 1989; Lauer and Simmons, 1988; McLaren, 1981; Darwinkel, 1978). The phenomenon of tiller death is often referred to as 'tiller dieback'. Late tillers (generally higher-order tillers) are the first to senesce as they are unfavorably placed, lower down in the canopy, where reduced light intensities and altered light quality restrict growth and development.

The cessation of tillering and the onset of tiller dieback often coincide with the specific stages of inflorescence development and main stem elongation (Baker and Gallagher, 1983). Tiller dieback is

highest among young tillers (Darwinkel, 1978,1979; Bremner, 1969), and is probably explained by the nutritional status of the main shoot and its daughter tillers (Masle-Meynard, 1981). During the period of tiller dieback, main stems become large sinks and reduce export, or even draw assimilates from the youngest tillers (Lauer and Simmons, 1988; Thorne and Wood, 1987).

In the field, additional factors are probably implicated in tiller dieback. Rising temperatures hasten leaf senescence, increase respiration and reduce the rate of net photosynthesis (Milthorpe and Moorby, 1979; Ford and Thorne, 1975). Leaf diseases such as Septoria leaf blotch and powdery mildew generally infect the lower canopy, reducing leaf area and producing toxins which accelerate senescence and interfere with the translocation of photoassimilates (King et al., 1983; Bainbridge, 1978). Water stress often accompanies higher temperatures. These factors may restrict root development in young tillers (Klepper et al., 1984; Masle-Meynard, 1981) so that water and nutrient uptake are seriously impaired during a period of drought stress.

2.5.2 Cultural Factors Affecting Tillering

2.5.2.1 Genotype

Genotype differences in the tillering capacity of different cereals have been noted by many researchers. However, cultivars which tiller profusely do not necessarily produce a great number of spikes. Differences in tillering capacity and final spike number have been attributed to plant height (Law et al., 1978), level of breeding and

selection (Bingham, 1978; Austin et al., 1980), and the presence of Rht genes in wheat (Gale, 1979). In general, dwarf- or semi-dwarf cultivars tiller more than tall cultivars, winter cereals tiller more than spring cereals, and two-rowed barley tillers more than six-rowed barley (Drawn from Stoskopf, 1985).

2.5.2.2 Seeding Density

Tillering is markedly affected by plant density. With decreasing sowing rate more tillers and spikes are produced per plant (Darwinkel, 1978; Bremner, 1969; Puckridge and Donald, 1967). However, tiller and spike numbers decline on a per unit area basis (McLaren, 1981; Darwinkel et al., 1977; Bremner, 1969a) since increases per plant cannot compensate fully for the lower seeding densities (McLaren, 1981). Plant competition is very apparent in dense stands. Fewer tillers are produced per plant, maximum tiller number is attained earlier (Darwinkel, 1978; Thorne and Blacklock, 1971) and tiller dieback commences sooner (Bremner, 1969b; McLaren, 1981). Percent shoot mortality is higher in denser populations (Thorne and Blacklock, 1971), especially with later-appearing tillers (Darwinkel, 1978).

2.5.2.3 Row Width

The effects of row width on cereal yield have been reviewed by Holliday (1963), who showed that plant populations were often confounded with spatial arrangement. However, in general, the number of tillers per plant increases with increasing row width, as does tiller survival (Watson and French, 1971). At the same seeding

density narrow rows have more shoots per unit area than wide rows, but higher tiller mortality can lead to spike numbers similar to those found in wide rows (Simmons et al., 1982). Fischer et al., (1976) observed that cultivars with erect leaves were slightly more tolerant of high plant densities, presumably because of a better distribution of light within the lower canopy.

2.5.2.4 Planting Date

The planting date of winter cereals determines the tiller and spike densities of a crop through its effects on plant winter survival (Smid and Jenkins, 1979), and shoot production in the fall and spring (Musick and Dusek, 1980; Darwinkel et al., 1977). Early planting promotes tillering in the fall (Thill et al., 1978; Darwinkel et al., 1977). Since the survival of a tiller is often related to its date of emergence, early planting leads to more spikes at harvest and to greater yields (Thill et al., 1978; Darwinkel et al., 1977). Musick and Dusek (1980) described a linear relationship between spike number and date of fall planting. However, in some environments no relationships are found among fall tiller numbers, spike numbers and yields (Smid and Jenkinson, 1979). Tillers differ in cold hardiness (Legge et al., 1983) so that not all tillers produced in the fall survive to bear spikes. With late fall planting, tillering occurs mostly in the spring and is accompanied by lower tiller survival (Prew et al., 1983). With spring cereals, late planting reduces tillering and can lead to a lower spike production.

2.5.2.5 Phytohormones

In many recent experiments, phytohormones have been shown to be implicated in the control of processes which govern the initiation of tiller buds, and their subsequent growth and development. The response of tillering and tiller survival to many agronomic practices and environmental conditions are no longer simply explained in terms of photoassimilate distribution within plants, but also in terms of specific hormone balances. In particular, the cytokinin/auxin ratio appears to control the dormancy of tiller buds, while GA governs their growth following release from dormancy (Woodward and Marshall, 1988; Leopold, 1949). Phytohormones or PGR definitely affect the pattern and dynamics of tillering, which will be discussed below (section 2.7).

2.5.2.6 Other Practices

The previous crop can influence tillering through its effects on soil structure, residual fertility, weed and disease control and water use. For example, continuous wheat cultivation has been observed to reduce spike numbers (Douglas et al., 1983) presumably by altering tiller production and/or survival. Scott et al. (1973) reported that underseeding white clover into wheat did not affect tiller production but did increase tiller survival, leading to higher spike numbers. Deep planting reduces tiller and spike numbers, possibly as a result of reduced coleoptilar tiller emergence (Frederick and Marshall, 1985; Masle-Meynard and Sebillotte, 1981).

2.5.3 Tillering in Relation to Yield

Generally, the relationship between grain yield and spike number is described as a 'flat-topped parabolic curve' (Darwinkel, 1978; Dougherty et al., 1978). This curve reflects the partitioning of yield into yield components which interact in response to genetic and environmental factors. Spike number is the first yield component to be established, followed by grain number per spike and then individual grain weight. Changes in one yield component can be compensated by changes in another later-established one. Thus, beyond a certain 'optimum' spike density, yields remain more or less stable over a wide range of spike densities because of reductions in grain number per spike or individual grain weight. However, until the critical or optimum spike number has been attained, higher yields per spike are unable to compensate for the initial low spike numbers, and high grain yields cannot be achieved (Nerson, 1980; Darwinkel, 1978). Research has focused on the understanding of factors which control tillering and tiller survival in order to alter the relationship between spike number and grain yield. It was hoped that increased yields can be obtained by higher spike densities (without the inevitable compensation by other yield components) or by increased productivity of surviving tillers in the absence of increased spike numbers.

The agronomic value of tillering has been debated by several researchers. Tiller spikes are less productive than those of the main shoot (Darwinkel, 1978; Darwinkel et al., 1977). Unproductive or sterile tillers are presumed to tie up nutrients and photoassimilates. Evapotranspiration by sterile tillers represents a non productive

water loss (Rawson and Donald, 1969) which can prevent adequate grain-filling in environments with low soil water reserves. Tillers have also been shown to have a negative influence on the growth and development of main shoots, as well as on their own yield components (Kirby and Jones, 1977; Kirby, 1974). Consequently, tillers have been considered wasteful (Kirby and Jones, 1977; Donald, 1968a,b) and parasitic (Rawson and Donald, 1969).

Radio tracer experiments have demonstrated that developing tillers are fully dependent upon parent shoots for nitrogen (Rawson and Donald, 1969), phosphorous (Greenway and Gunn, 1966) and fixed carbon (Rawson and Hofstra, 1969), and that they can import appreciable amounts of carbohydrates and nutrients from their parent shoots. However, the reverse can be true, in that main stems are able to obtain assimilates from dying tillers (Lauer and Simmons, 1988; Donnelly et al., 1983; Bunting and Drennan, 1966), although this is not always true (Thorne and Wood, 1987). As a result, it has been suggested that sterile tillers act as a temporary reservoir for productive shoots (Palfi and Deszi, 1960). However, the amount of nutrients and fixed carbon translocated from higher order tillers to main stems and primary tillers is generally negligible, so that the reservoir potential of tillers is likely to be insignificant.

The removal of tillers or tiller buds often increases the growth rate and the size of main shoots (Kirby and Jones, 1975, 1977), grain and straw yields (Mohamed and Marshall, 1979) and grain nitrogen concentration (Mohamed and Marshall, 1979; Kirby and Jones, 1977). Tiller removal in barley accelerates leaf emergence, increases leaf

size and occasionally leaf number (Kirby and Jones, 1975, 1977). Tinker and Jones (1931) found that complete tiller removal increased the growth rate of the main shoot, especially at lower densities where plants generally produce more tillers. Detillering treatments applied early produce the greatest responses (Mohamed and Marshall, 1979; Kemp and Whingwiri, 1980). Increases in grain yield result from improved grain set and grain weight (Kirby and Jones, 1977; Dougherty et al., 1975). Enhanced survival of spikelet primordia have also been observed (Ford and Thorne, 1975). In field experiments, however, Borojevic and Kraljevic-Balalic (1980) reported that a detillering treatment led to reductions in spike length and spike fertility. However, it is possible that the reductions they observed resulted from increased respiration due to wounding caused by incomplete or partial detillering (i.e. defoliation). Defoliated tillers have been shown to compete with main shoots in both oat and barley (Gu and Marshall, 1988).

In a series of pot experiments involving different shoot arrangements per plant and per pot, Donald (1968b) demonstrated the superiority of uniculms over multiculms in crowded situations, from which he developed the concept of a uniculm ideotype in which tillers are absent (Donald, 1968a). In a crop composed of uniculm plants, grain yields are secured from the higher-yielding, main stem spikes, which in the absence of competition from tillers, are expected to yield even more. However, it appears that compensation among yield components also exists among uniculms.

Tillering is an important trait of cereals and other grasses,

allowing plants to make the most of their surrounding environment, and enabling them to compensate for poor establishment or uncontrollable losses early in the season. It is unlikely that such compensation could be obtained from uniculms, and the higher rate of seeding necessary to produce optimum spike densities make uniculms even less desirable. The alternative, which has been adopted by some breeders, is the development of cultivars characterized by reduced tiller numbers with synchronous development. Thus, tillering can be manipulated to increase the number of spikes produced. However, the relationship between spike number and grain yield appears to be very sensitive to environmental factors, so that a relationship between tiller production and grain yield is not always present. There appears to be a potential for altering plant type with the use of plant growth regulators. For example, Matthews and Caldicott (1981) demonstrated that CCC-treated barley plants had greater within-plant uniformity both in tiller-spike size and grain size within a spike. More discussion on this is found below (section 2.7).

As for the usefulness of tillers, even though they have been shown to compete with main spikes, in certain environments they can, as a group, contribute significantly to yield. This, along with the insurance tillering provides early in the season, and anticipated higher seeding costs of uniculm or biculm cultivars still make tillering a valuable characteristic of small grain cereals in modern agriculture. Care must be taken, however, to avoid situations where excessive tillering occurs, as these are known to be harmful to yield.

2.6 Lodging

Lodging in small grain cereals has long been responsible for reductions in grain yield and quality. Lodging can result in direct yield losses by reducing photosynthesis and in indirect yield losses by promoting conditions conducive to mold and disease, and increasing harvest difficulty and harvest losses (Stoskopf, 1985). Generally speaking, barley is more susceptible to lodging than any other cereal except oat. Time of lodging occurrence and the severity of lodging are the determinants of the yield loss.

In general, lodging near the time of heading is the most detrimental for both barley (Stanca et al., 1979; Sisler and Olson, 1951) and wheat (Weibel and Pendleton, 1964). For example, studying the effect of time of occurrence and the degree of lodging on barley in artificially lodged plots, Sisler and Olson (1951) demonstrated that severe reductions in grain yield and 1000-grain weight were found in the earlier lodging treatments, this is during the period from heading to maturity. Spring barley yield was decreased by an average of 38 % when lodging occurred near heading; however, it was decreased only 22 % when lodging occurred 20 days later (Stanca et at., 1979). Lodging before anthesis is less serious because newly elongating internodes recover by bending upwards due to a negative geotropic response (Stoskopf, 1985). Complete lodging reduced yield much more than lodging to a 45^0 angle, regardless the growth stage when lodging was induced (Sisler and Olson, 1951).

2.7 Morphoregulators and Plant Growth

The idea of using plant hormones to improve the growth and development of crop plants is not new. The possibility first arose in the 1930s with the discovery of auxins as natural plant hormones. Synthetic IAA first became available for horticultural use in 1936, to be followed by a-naphthyl acetic acid (NAA) and, in 1940s, by the herbicidal auxins 2,4-dichlorol phenoxy acetic acid (2,4-D) and 4-chloro-2-methyl phenoxy acetic acid (MCPA). Later, with the recognition of GAs, in the early 1950s, and cytokinins and ethylene in the early 1960s, more and more synthetic growth regulators have been identified, produced and commercially tested. At this time numerous different growth regulators are used in horticultural and agronomic crop production. Depending on the functions PGR possess, similarity and antagonism to the natural plant hormones, the following discussion is focused on synthetic plant growth regulators which have been tested and utilized in agriculture production.

2.7.1 Auxins

Growth regulators such as TIBA (2,3,4-triiodobenzoic acid), which characteristically inhibit the basipetal transport of auxin (Niedergang-Kamien and Skoog, 1956), can cause the lateral buds (tillers in cereals) to be released from dormancy and grow out into side shoots (Luckwill, 1981). In experiments with spring barley, Leopold (1949) found that application of the anti-auxin TIBA decreased the apical dominance of the main stems, thereby increasing tillering. A similar response to TIBA was also reported for spring wheat (Jewiss,

1972).

TIBA was commercially released in 1961 as a product for the enhancement of fruit bud formation and for widening the branch angle in certain varieties of apple. Unlike 2,4-D or NAA, TIBA is a compound with an antagonistic activity of auxins (Jung, 1984).

It has reported that in vegetables and fruit crops, TIBA is effective as a male sterilant without seriously depressing ovule fertility (Iyer and Randawa, 1965), which could make it a useful tool for hybrid seed production for horticultural applications.

2.7.2 Gibberellins and the Antagonists

Gibberellic acid (GA) treatment of cereals promotes the extension of actively growing tiller buds, but restricts the growth of others (Sharif and Dale, 1980b). Tillers apparently require a certain degree of vascular connection with the axial stele for GA to be effective. Thus, tillers which have not yet emerged from the leaf sheath are likely to be inhibited (Hutley-Bull and Schwabe, 1982, 1980).

GA treatments applied to barley and wheat plants in controlled environments and field experiments have been shown to restrict tiller numbers (Hutley-Bull and Schwabe, 1982; Batch et al., 1980; Johnston and Jeffcoat, 1977; Jewiss, 1972). Plant genotype in wheat can alter the response dramatically (Gale, 1978; Gale and Marshall, 1973a,b). Tall cultivars are sensitive to GA, with inhibition of tillering following GA treatment. Semi-dwarf cultivars react in an opposite manner, and tiller profusely. Thus, in tall cultivars, GA promotes the stem extension and development of the main shoot and early emerged

tillers, but inhibits the emergence and growth of higher-order tillers (Hutley-Bull and Schwabe, 1980). Greater tiller survival and within-plant uniformity are the result of suppressed tillering (Koranteng and Matthews, 1982; Batch et al., 1980).

Anti-gibberellins are chemical compounds that inhibit gibberellin biosynthesis and/or activity. They are mainly composed of onium compounds (CCC, mepiquat chloride (DPC), N-dimethyl-N-ß-chloroethyl-hydrazonium chloride (CMH)), pyrimidine derivatives (ancymidol) and norbornendodiazetine derivatives (Tetcyclacis = NDA). Anti-gibberellins are very important chemicals in agronomic and and horticultural crops. In fact, CCC is one of the three growth regulators (CCC, ethephon, and DPC) that are most widely used in cereal crop production (Jung and Rademacher, 1983). Therefore, attention will be given to the mechanisms of anti-gibberellin chemicals, especially the mode of action of CCC.

CCC was first described by Tolbert in 1960 as being active as a growth retardant on wheat (Tolbert, 1960a,b). Its anti-gibberillin action can be explained in terms of inhibition of cyclization of trans-geranyl-geranyl-pyrophosphate, which leads to a low concentration of kaurene (a GA_3 precursor), thereby, the levels of endogenous gibberellins are reduced by inhibiting their biosynthesis (Jung, 1984) and plant height by slowing both cell division and elongation. Although CCC was considered unreliable for reducing height and lodging control in barley, due to poor absorption of CCC and rapid transported within the barley plant after absorption (Skopik and Cervinka, 1967), its ability to manipulate the growth and

development of tillers stimulated the investigation of its potential use in spring barley. Alcock et al. (1966) demonstrated that ^{11}C-labeled CCC moved more slowly in barley than in wheat. This PGR may reduce the apical dominance of the main stem and thus lead to more tillers per plant or per unit area and greater number of spike-bearing tillers in winter and spring barley (Waddington and Cartwright, 1986; Matthews et al., 1981; Bokhari and Younger, 1971). CCC, an anti-gibberellin chemical, can shorten and strengthen the basal internode of cereals via inhibiting cell division and cell expansion in the sub-apical region of the stem, usually without similarly affecting the apical meristem (Dicks, 1980; Weaver, 1972). This internode shortening can often be reversed by treating the plant with gibberellin, suggesting that the growth retardant functions by inhibiting gibberellin biosynthesis (Luckwill, 1981). Used primarily to increase resistance to lodging (Humphries, 1968), it does, however, accelerate the appearance and early growth of tillers in wheat and barley (Koranteng and Matthews, 1982; Matthews et al., 1981; Stamp and Geisler, 1976). Total tiller numbers, however, may remain unaffected (Kettlewell et al., 1983). Since lodging prevents late-appearing tillers from developing spikes (Syme, 1968), chlormequat may increase spike numbers by allowing the survival of higher-order tillers positioned lower down in the canopy. It is possible that Bettaquat, a formulation of chlormequat, improves tiller survival by synchronizing tiller production (Williams et al., 1982). Chlormequat has been shown to increase the survival probability of secondary tillers in barley by hastening their appearance and by increasing their size (Matthews et

al., 1981). Thus, CCC increases spike number and yield by favoring the survival of late, higher-order tillers without affecting mainstem and primary tiller yields. Gibberellins, on the other hand, limit spike production but reduces the hierarchical relationship between the main shoot and its tillers. The effects of chlormequat on grain yield and its yield components in the absence of lodging has been reviewed by Green (1986), while effects on the growth and development of winter barley have been reviewed by Naylor et al. (1987).

The primary use of CCC is to prevent lodging in wheat. In Germany, by far the greatest part of the area under wheat cultivation has been treated with CCC for many years. As in a number of other European countries, this plant growth regulator is an integral element of the wheat production system. In the UK, CCC is used extensively on barley and wheat to regulate tiller growth rate. The primary and secondary tillers are arrested temporarily. This lessens their dominance over higher-order tillers, and thereby distributes growth and yield more evenly among tillers and increases total yield (Gardner et al., 1985).

Mepiquat chloride (DPC) is used in cotton to suppress vegetative growth by reducing the main stem and fruiting branch internode lengths (York, 1983). The effects on yield have been inconsistent. Reported responses including yield increase (Kerby, 1985), yield reduction (Crawford, 1981), and no yield effect (Stuart et al., 1984).

Ancymidol reduces internode elongation in a wide range of species. It has been evaluated on a range of commercial greenhouse plants including many varieties of chrysanthemum, poinsettia, dahlia,

tulip, Easter lily and other ornamentals with excellent results (Thomas, 1982). Ancymidol inhibits gibberellin-induced growth and thus elicits other effects such as increased stem diameter (Montague, 1975) and increased root initiation in shoot cuttings (Kefford, 1973).

Paclobutrazol is a new trazole type growth retardant that inhibits GA biosynthesis in plants by blocking kaurene oxidase, thus inhibiting the oxidation of kaurene to kaurenic acid (Dalziel and Lawrence, 1984). It reduces endogenous ABA levels (Wang et al., 1987) and inhibits shoot growth of apple trees (Quinlan and Richardson, 1984). Paclobutrazol was also reported to reduce plant height, leaf area, shoot fresh weight and dry weight, and evapotranspiration, improve yield and quality of apple fruits (Williams, 1984), control shoot length of chrysanthemum and lily at low concentrations (Thomas, 1982), and prevent lodging in rice (Eastin, 1983) but did not affect leaf diffusive resistance or the components of leaf water potential of sunflower (Helianthus annuus L.) (Shanahan and Nielsen, 1987; Wample and Culver, 1983). While the commercial use of CCC has been mainly restricted to cereals paclobutrazol is being extensively used in the horticultural industry to regulate the growth of fruit trees and ornamentals (Roberts and Hooley, 1988).

The main effect of growth retardant treatments is to reduce the dominance of the main stem (Isbell and Morgan, 1982), thus encouraging the development of more florets and the faster growth of spikes in later formed shoots (Waddington et al., 1986).

2.7.3 Cytokinins

Commonly used synthetic cytokinins are N^6-benzyladenine (BA), Kinetin, purin-6-yl (tetra-hydropyran-2-yl) amine (PBA). Exogenously applied cytokinins promote tiller bud growth in cereals (Harrison and Kaufman, 1980; Langer et al., 1973). In field cereal production, cytokinins have been shown to promote tiller bud growth (Harrison and Kaufman, 1980). Williams and Cartwright (1980) demonstrated that application of BA during the tillering stage synchronized tiller development so that grain yield was increased due to an increase in spike-bearing shoots and a reduction in spikelet abortion. Johnston and Jeffcoat (1977) reported that 2 different cytokinins increased overall tillering but produced fewer spikes because of increased competition. However, Sharif and Dale (1980a) demonstrated that cytokinins were not only required for the release of tiller bud inhibition, but also for their subsequent growth.

2.7.4 Ethylene

Ethylene was first used to 'degreen' citrus in 1924 (Morgan, 1986), but was not widely used as a plant growth regulator until after the development of ethephon during the 1960s. Of the currently known hormones in plants, ethylene is the most widely and successfully used in agriculture (Roberts and Hooley, 1988; Morgan, 1986). Ethephon is a synthetic growth regulator that releases ethylene slowly inside plant tissues through a pH-dependent reaction (Warner and Leopold, 1969). Ethylene interferes with auxin biosynthesis and with transport in stem tissues (Evan, 1984), thereby reducing auxin's ability to

promote stem elongation and to inhibit tiller bud outgrowth (Woodward and Marshall, 1987). Many studies have shown that ethephon can prevent plant lodging in a variety of species (Dahnous et al., 1982) via an inhibition of stem elongation (Sachs and Hachett, 1972), which leads to reduced plant height.

The use of ethephon tends to shorten and stiffen ear-bearing culms and results in less lodging. Ethephon has been used in Europe to reduce plant height and control lodging. Many North American trials on spring wheat and barley show that ethephon is effective in lodging control and in realizing more of the maximum yield potential (Caldwell et al., 1988; Dahnous et al., 1982). However, positive and negative grain yield responses to ethephon have been reported even when no lodging occurred in comparable untreated barley (Moes and Stobbe, 1991a; Caldwell et al., 1988; Simmons et al., 1988; Dahnous et al., 1982). In addition to reducing lodging, ethephon applied to cereals may affect yield via altering individual yield components either positively or negatively (Moes and Stobbe, 1991b). Ethephon treatment increased the number of spikes m^{-2} in spring barley (Moes and Stobbe, 1991b; Simmons et al., 1988), winter barley (Hill et al., 1982) and spring wheat (Simmons et al., 1988). The increased spike number has been accompanied with improved grain yield even in the absence of lodging (Hill et al., 1982). Yet, ethephon often decreased grain number per spike, and/or 1000-grain weight (Moes and Stobbe, 1991c). The various responses to ethephon may be due to genotypic sensitivities (Caldwell, 1988), environmental conditions (Wiesma et al., 1986) or both (Caldwell et al., 1988). In continental climatic conditions such as the

Prairie Provinces of Canada, the potential for ethephon to induce late tillering and/or cause yield reductions restricts the use of ethephon in the situations where the risk of severe lodging can be high (Foster et al., 1991; Moes and Stobbe, 1991a).

Preface to Section 3

Section 3 is the material contained in a manuscript by Ma and Smith (1991a) accepted with revision for publication in the journal Crop Science. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table or figure is presented at the end of the section.

In this section we address the timing and duration of each stage of main-stem apical development as well as the pattern and dynamics of spikelet primordium production under continental field conditions.

Section 3

APICAL DEVELOPMENT OF SPRING BARLEY UNDER FIELD CONDITIONS IN QUEBEC

3.1 Abstract

Although the apical development of barley (Hordeum vulgare L.) has been extensively researched, a complete description of spring barley apical development stages has not been published for continental North American field conditions. This study determined the timing and duration of the apical development stages, and the pattern and dynamics of spikelet primordium initiation. Data were collected for two barley cultivars for three successive seasons in eastern Canada. From the seedling stage to anthesis, apical development and the total number of leaf and spikelet primordia were monitored, and both were related to days after seeding (DAS) and to accumulated growing degree-days (AGDD). The main-stem apex reached the double ridge stage 22 to 24 DAS (320 to 340 AGDD), awn initiation 40 to 42 DAS (approximately 650 AGDD), and anthesis 50 to 56 DAS (860 to 940 AGDD), with some variations among cultivars and years. Nine main-stem leaf primordia were initiated by 16 DAS. Primordium initiation was completed by awn initiation when 40 to 44 primordia had been formed. The data provide a description of barley apical development stages and indicate that spikelet primordium production 1) occurred in three distinct stages with different rates of development, 2) was largely a function of thermal time, although genotype and climatic factors may have some effect, and 3) was related to time or thermal time in a curvilinear,

rather than a linear fashion as indicated in previously published reports.

3.2 Introduction

The stages of barley (Hordeum vulgare L.) apical development were determined under controlled conditions by Bonnett (1966). Kirby and Appleyard (1981) presented valuable photographic plates and diagrams with detailed descriptions of each apex developmental stage for both wheat (Triticum aestivum L.) and barley. Most recent studies have been conducted under controlled conditions and/or concentrated on specific segments or events in the process of apical development. For example, Cao and Moss (1989a, 1989b) demonstrated that main stem leaf emergence is a linear function of accumulated growing-degree days and daylength. Controlled environmental studies show that the interaction between temerapture and daylength has a large impact on leaf emergence and expansion (Cao and Moss, 1989c), spikelet primordia initiation, and apical development (Wright and Hughes, 1987). Under field conditions, temperature and daylength are often confounded, particularly when seeding date is changed. Thus, controlled-environment data or data from field studies conducted under a given set of climatic conditions are unlikely to apply under a different set of field conditions, particularly if the conditions are very different. Little published information is available regarding timing and duration of barley apical development stages under field conditions in North America.

Apical development of spring barley is a continuous process.

The maximum potential number of grains per spike is set at the cessation of apical development. Normally, 10 to 12 spikelets at the tip of the apex die (Kirby and Rymer, 1974) because of competition for nutrients (Kirby and Faris, 1970). Both environmental and managerial factors can influence the rate and total number of primordia formed in the spike, and therefore the timing and duration of apical development.

Barley is a quantitative long-day plant. It is well known that daylength and temperature strongly affect barley apical development. Much faster rates of spikelet initiation and development were found to occur under long days than under short days (Aspinall and Paleg, 1963; Cottrell and Dale, 1986). Cottrell and Dale (1986) demonstrated that barley plants under an 8 h photoperiod initiated many more spikelets, but did so at a lower rate than those under a 16 h photoperiod. Wright and Hughes (1987) showed that delaying the sowing of spring barley, which resulted in spikelet initiation and development under higher temperature and longer daylength conditions, accelerated the development of primordia and shortened the duration of all stages of apical development. On the other hand, spikelet primordium initiation was slower at lower temperatures, but the initiation phase lasted longer. Thus, main stem apices initiated a similar number of spikelet primordia at both high and low temperatures (Russell et al., 1982). Plant population density influenced the time required for the apex to reach successive development stages. At 800 plants m^{-2} or higher, the apex reached double ridge stage earlier than at a more normal density (400 plants m^{-2}). This difference persisted throughout the subsequent

development of the apex (Kirby and Faris, 1970). When plants were under water-deficit stress, fewer total primordia were initiated and the rate of initiation was slower (Nicholls and May, 1963).

Under reasonable growing conditions the same sequence of developmental stages will occur at any location; however, the times and durations of barley apical development stages that have been measured under either controlled (Nicholls and May, 1963) or European field conditions (Kirby and Farris, 1970; Kirby and Appleyard, 1981) are unlikely to apply to North American field conditions. In the case of controlled-environment studies, the growth regimes often entail fixed combinations of factors or abrupt changes in conditions that plants would not experience under a field regime (Baker and Gallagher, 1983). Plants grown in Europe experience very different environmental conditions than those grown in North America. Most of North America is continental in climate, with even the east coast experiencing a modified continental climate, while northern Europe generally experiences a maritime climate with lower temperature, longer daylength and greater precipitation during spring barley growing season. The duration of the apical development in spring barley should be much longer in Europe than in north-eastern North America. Russell et al. (1982) reported that it took 70 to 80 d for spring barley to reach heading under conditions prevailing at the Scottish Crop Research Institute. In Quebec heading of spring barley usually occurs about 50 days after seeding. Moreover, there is no published information available regarding the relationships between the apex stages and thermal time.

Understanding the effects of climatic change on the timing and duration of apical development of barley is essential for understanding and predicting its development, and for providing information that could be used to develop practical crop management techniques. Currently, several agronomic practices, such as application of some herbicides or growth regulators, may have optimal effects only when applied at a specific development stage (Kirby and Appleyard, 1982; Kirby et al., 1985). In this paper timing and duration of all main stem apical development stages are reported for spring barley produced under North American field conditions. The patterns of spikelet primordium production on the main stem are also discussed in relation to days after seeding (DAS) and accumulated growing-degree days (AGDD).

3.3 Materials and Methods

The same experiment was conducted during 1987, 1988 and 1989, on Bearbrook clay soil (fine, mixed, nonacid mesic Humaquept), at the Emile A. Lods Agronomy Research Center, Macdonald College of McGill University, Quebec, Canada. Three hundred kg ha^{-1} of 5-9-17 NPK commercial compound fertilizer were applied to the site prior to seeding. Two spring barley cultivars, Cadette (a semidwarf lodging-resistant type) and Leger (a standard lodging-susceptible type) with the similar maturity dates (Cadette can be 1 d later than Leger) (Agriculture Canada, Food Production and Inspection Branch, Registration No. 2711 and No. 2237, respectively) were grown in field

plots with four replicates. Plots (4.4 by 2.2 m) were seeded at a rate of 450 seeds m^{-2} in rows spaced 10 cm apart. Seeding took place on 3 May in 1987 and 1988, and on 1 May 1989. Immediately after seeding, 100 kg N ha^{-1}, as ammonium nitrate, were broadcast onto each plot. A mixture of 280 g a.i. ha^{-1} of bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) and 646 g a.i. ha^{-1} of diclofop-methyl (methyl 2 - (4- (2, 4 - dichlorophenoxy) phenoxy) proponate) was applied at Zadoks' growth stage 12 (Zadoks et al., 1974) to control weeds.

Plants were sampled every 2 days from approximately 15 DAS until the awn initial stage. By 15 DAS the second leaf of the main stem was emerging on most plants. Work of Kirby and Appleyard (1981) demonstrated that the maximum number of leaf and spikelet primordia have been formed when the apex reaches the awn initial stage, and after this stage morphological changes in the spike occurred more slowly. For these reasons the sampling interval was lengthened to every 4 days after the awn initial stage had been reached.

At each sampling date, three consecutive plants were randomly selected from areas of full, even establishment within one of the central rows of each plot. Observations were confined to the main shoot. The main stem apex was dissected and the stage was taken to be that of the most advanced primordia on the apex (Aspinall and Paleg, 1963). The key stages of apex development were determined according to the descriptions of Kirby and Appleyard (1981). These stages were: vegetative (VS), double ridge (DR), triple mound (TR), glume initial (GL), lemma initial (LE), stamen initial (ST), awn initial (AW) and anthesis (AN).

At each sampling the number of accumulated primordia was determined from the first leaf to the last recognizable primordium by summing the number of developed leaves, leaf primordia and/or spikelet primordia. When both a leaf primordium and a spikelet primordium could be distinguished at a single node, viz. double ridge stage, the paired structure was counted as a single primordium. When spikelet triplets appeared, each triplet was counted as single primordium (Kirby and Faris, 1970). Accumulated total spikelet primordia (TP) was calculated as the difference of the total primordia and leaf and leaf primordium numbers (usually 9 leaves formed on the main stem in this study).

Rainfall and temperature data were collected at the meteorological station of the Emile A. Lods Agronomy Research Center, approximately 500 m from the experimental site.

The times required to reach each of the major stages of apical development were reported as means of DAS $\pm$ one standard deviation. Apical development was also related to thermal time: accumulated growing degree-days (AGDD) was calculated from seeding with a base temperature of $0^{o}C$ (Gallagher, 1979; Baker et al., 1980; Cao and Moss, 1989a). This was calculated as

$$AGDD = \Sigma[(T_{max} + T_{min}) / 2]$$

T_{max} and T_{min} were daily maximum and minimum temperatures and respectively restricted to greater than or equal to $0^{o}C$. Analysis of variance (Steel and Torrie, 1980) on the overall processes of apical development, as affected by either time or thermal time, was not performed because of the non-linearity of the scale for the apex

stages (Aspinall and Paleg, 1963). Data of TP were always selected to include only the actual period of spikelet formation (from 15 DAS to the appearance of maximum value of TP for each cultivar). The relationships between TP and calendar time or thermal time was analyzed with the GLM procedure (SAS Institute, 1985). Curvilinear regressions of TP over DAS or AGDD were performed according to Steel and Torrie (1980).

3.4 Results and Discussion

Accumulated rainfall, average maximum and minimum temperatures and AGDD for 6 successive 10-d periods after seeding and the 15-yr averages for these parameters are presented in Table 3.1. These parameters, particularly early season rainfall varied considerably among years.

Apex Development

The main-stem-double-ridge stage was reached almost simultaneously in the two cultivars, with Leger being less than 1 d ahead of Cadette (Table 3.2). Between the double ridge and awn initiation stages Leger retained a small (1 d or less) lead over Cadette, but from awn initiation to anthesis this difference increased to 3 d. Thus, Cadette anthesis was 2 to 3 days after Leger. These genotypic differences within a species in the course of apical development are of interest. It might be possible to manipulate yield components independently of each other by either cultural practices such as application of plant growth regulators or nutrients at different phase

of development, or via breeding effort to select distinct period of given apical stage for a specific locale. In a field study, Kitchen and Rasmusson (1983) found that variations existed among barley genotypes in the duration of leaf initiation, spike initiation and spike growth, however, there was no data available on the dynamics of apical development, particularly under North American field conditions.

In all three years, an interval of approximately 30 d for Leger and 31 to 33 d for Cadette elapsed between the double ridge and anthesis stages. The slight variation among years for the time elapsed between the double ridge and anthesis stages may have been caused by differences in climatic conditions between years (Table 3.1). This is in agreement with Wright and Hughes (1987), who found that the climatic regime experienced by a spring barley crop affected the number of days from seeding to each stage of apical development.

In 1987 and 1989, the main-stem apices of both cultivars reached the double ridge stage at 22 to 24 DAS (320 to 340 AGDD). Expressed as a function of DAS, double ridge structures were formed earlier in 1988 than in 1987 or 1989. These differences among years were greatly reduced but not removed when the data were expressed as AGDD. Below normal rainfall in 1988 (Section 7; Table 3.1) may have accelerated apex development in that year compared to 1987 and 1989, even when expressed as a function of AGDD. Water stress has been found to affect spikelet initiation and apex development (Nicholls and May, 1963). In the two years with more normal rainfall, lemma primordia, the first recognizable barley floret structures to appear, were

initiated 29 to 32 DAS (450 to 470 AGDD). Awn initiation occurred when the number of primordia reached its maximum value, 40 to 44 DAS (650 to 680 AGDD). Anthesis occurred 53 DAS (860 AGDD) for Leger and 56 DAS (940 AGDD) for Cadette.

In Quebec, the apical development of spring barley is compressed into a relatively short period. The entire process, from seeding to anthesis, took approximately 55 d (860 to 940 AGDD) under field conditions, and approximately 30 d elapsed between the double ridge and anthesis stages (Table 3.2). Our observations differ from European data (e.g. Kirby and Faris, 1970; Kirby and Appleyard, 1981; Russell et al., 1982), where the apical development of spring barley lasts 10 to 20 d longer. For instance, Kirby and Appleyard (1981) stated that it took approximately 50 d for spring barley to reach awn primordium stage. The European growing season is cooler and longer than that of north eastern North America, where the climate is generally continental. Thus, our data are more applicable to barley grown under North American continental conditions.

Understanding the impact of climate differences on the processes of apical development allows accurate recommendations regarding the application of agrochemicals such as hormone-type herbicides or growth regulators. For instance, in 1988, hot weather and below normal rainfall early in the season (Table 3.1) shortened the time required for the main-stem apex to reach specific stages (Table 3.2). The external morphology was less affected. When the 3rd leaf was fully expanded, i.e. Zadoks' growth stage 13, the main-stem apex for the most developed plant was at the double ridge stage in 1987, and at the

lemma initial in 1988.

Primordia Production

By approximately 16 DAS, when sampling commenced, both Leger and Cadette had initiated all leaf primordia (9 leaves were ultimately formed on the main stem in each year of this 3-year study). One leaf was fully expanded and 1 to 2 more leaves were visible (leaf blade longer than 0.5 cm before dissection).

The period from the completion of leaf initiation to the appearance of maximum number of total primordia on the main stem represented spikelet initiation. This process lasted 20 to 25 d depending largely on yearly environmental changes and slightly on genotype differences. The relationships between the accumulated number of main-stem spikelet primordia and DAS or AGDD were curvilinear (Table 3.3). Yearly variations were always significant, even when AGDD was the independent variable; this indicates that separate models are required for each year (Figs 3.1 and 3.2).

Spikelet primordia production was a quadratic function of DAS, and of AGDD in all years. The R^2 values for these relationships were always greater than 0.9 for DAS, and always greater than or equal to 0.96 for AGDD. Fitting other relationships such as linear, sigmoidal or logarithmic functions were also attempted; however, the quadratic function fit best. In 1987, the TP production was clearly in distinct phases, each with its own rate of primordia production (Figs 3.1 and 3.2). From 16 to 25 DAS, the phase change from vegetative to reproductive apex the rate of spikelet primordium initiation were

relatively slow. From 25 to 32 DAS, the period of spikelet formation and differentiation, the rate of spikelet primordia initiation was dramatically increased. Thereafter, the TP production proceeded more slowly, and eventually ceased at about awn initiation (approximately 40 DAS). In 1988 and 1989 more warm and/or dry conditions occurred early in the growing season (Table 3.1). The initiation of spikelet primordia was fast once the completion of leaf primordia formation. Subsequently, the pattern was similar to that observed in 1987, but the maximum number of spikelet primordia was reached earlier. These observations generally agreed with those of Kirby and Appleyard (1981), although our data indicate a higher rate of spikelet initiation, and a shorter duration of each phase. In all years of this study approximately 30 to 35 spikelet primordia were formed, each developing into 3 spikelets. In Great Britain, typically 40 spikelet primordia are formed in about 50 DAS (Kirby and Appleyard, 1981). Presumably this is due to the differences between the climatic conditions in North America and those of Europe, and to differences between cultivars grown in these regions.

Previous studies of barley and other cereals have indicated that TP or spikelet primordia production was a linear function of thermal time (Baker and Gallagher, 1983; Hunt and Chapleau, 1986; Jones and Allen, 1986). Our data indicated that TP was a nonlinear function of time or thermal time (Table 3.3), indicating that spikelet initiation on the main stem was a heterogeneous process under field conditions. Working on winter cereals, Hunt and Chapleau (1986) also found that under field conditions primordia production was distinctly lower

earlier in the season in one of the 2 year studied and reported that linear relationship primordia and thermal time did not fit in that year. An explanation for the nonlinear relationship may lie in the distinct phases of spikelet primordium production as discussed above. In addition, the major sink in the developing spike may shift from time to time. For instance, during the transition period the metabolism may change and the initial spikelet primordia may be formed rather slowly. During the double ridge stage, new primordia are the primary sinks, the rate of initiation is fast. Later, when lemma or stamens start to initiate, the lower part of the central inflorescence is the primary sink, and the formation of spikelet primordia on the tip is slow. Thus it is reasonable to consider the whole process of the TP production and dynamics as a nonlinear function of time.

In summary, our data illustrate: 1) the times and durations of key stages of apical development of spring barley grown in the field in a North American continental climate and the thermal time requirement to reach these stages, 2) that apical development and primordia production relate to thermal time better than to time alone, 3) the relationship between thermal time and the TP rate is quadratic, and 4) apical development occurs more rapidly under the conditions in which this research was conducted, than under those in which previously reported field work was carried out. Modeling and prediction of barley growth and development requires such detailed data on apical development.

Table 3.1. Accumulated rainfall (R) in millimeters, average maximum (MaT) and minimum (MiT) temperatures (^{o}C) and accumulated growing degree-days (AGDD) for 6 successive 10-d periods after seeding.

	Year												15-yr			
10-d	1987				1988				1989				Average[1]			
Periods	R	MaT	MiT	AGDD	R	MaT	MiT	AGDD	R	MaT	MiT	AGDD	R	MaT	MiT	AGDD
0 - 9	20	16	5	100	0	24	10	145	41	17	5	96	25	17	5	111
10 - 19	36	18	7	223	27	20	9	290	57	25	11	274	42	21	9	260
20 - 29	72	23	14	406	43	24	12	469	83	24	12	450	66	23	11	429
30 - 39	153	22	14	585	44	22	9	623	94	24	12	633	92	23	11	598
40 - 49	164	24	13	769	45	30	16	856	168	21	10	785	127	25	14	790
50 - 59	187	24	16	967	125	20	11	1013	175	23	12	1011	158	26	15	992

[1] All the parameters were calculated starting from 1 May, and are averaged for the years 1975 through 1989.

Table 3.2. Number of days after seeding (DAS) or accumulated growing degree-days (AGDD) to achieve each main stem apical development stages.

	DAS			AGDD		
STAGE	1987	1988	1989	1987	1988	1989
			CADETTE			
DR†	24.7 (0.2)‡	22.0 (0.2)	22.7 (0.4)	321 (4.2)	335 (3.2)	342 (6.7)
TM	30.0 (0.1)	24.9 (0.4)	26.5 (0.1)	436 (1.0)	401 (7.7)	427 (5.0)
LE	32.0 (0 3)	27.2 (0.2)	29.2 (0.2)	470 (5.0)	441 (3.5)	465 (4.7)
ST	33.5 (0.4)	29.3 (0.3)	31.6 (0.2)	495 (7.2)	480 (4.7)	501 (0.9)
AW	43.7 (0.7)	38.6 (0.4)	42.5 (0.6)	678 (12.7)	639 (7.5)	689 (8.0)
AN	56.5 (0.5)	51.2 (1.5)	56.0 (0.7)	935 (10.5)	904 (15.4)	943 (6.0)
			LEGER			
DR	23.8 (0.5)	20.7 (0.2)	22.1 (0.3)	312 (7.8)	329 (3.0)	331 (5.5)
TM	29.4 (0.4)	22.9 (0.2)	25.7 (0.9)	413 (8.6)	361 (3.8)	419 (15.0)
LE	31.1 (0.3)	25.5 (0.5)	29.0 (0.3)	447 (6.5)	413 (7.7)	453 (4.2)
ST	33.0 (0.3)	27.3 (0.4)	30.9 (0.0)	485 (5.6)	447 (7.2)	498 (3.0)
AW	42.0 (0.7)	38.0 (0.4)	40.0 (0.6)	648 (12.5)	628 (7.4)	654 (9.2)
AN	53.0 (0.3)	49.0 (1.3)	52.5 (0.9)	859 (4.5)	857 (3.5)	865 (5.1)

† Apical development stages: DR = double ridge, TM = triple mound, LE = lemma initial, ST = stamen initial, AW = awn initial, AN = anthesis.

‡ Values are means of at least 12 samples (± standard deviation).

Table 3.3. Mean squares from analyses of covariance to determine the relationships between total primordia of the main stem and DAS, or AGDD. Data included in the analysis were from 15 DAS to the date of maximum number of spikelet primordia (usually 38 to 40 DAS).

		Total primordia	
Source	DF	DAS	AGDD
Year (Y)	2	166.0***	121.1***
Cultivar(C)	1	0.5	0.1
Y * C	2	1.0	2.3
X†	1	803.9***	935.4***
X * X	1	412.6***	431.5***
Error	63	6.0	4.03
R^2	-	0.95	0.96
CV	-	11.8	9.7

† Independent variable (i.e. DAS, AGDD)

*** Significant at the 0.001 level of probability.

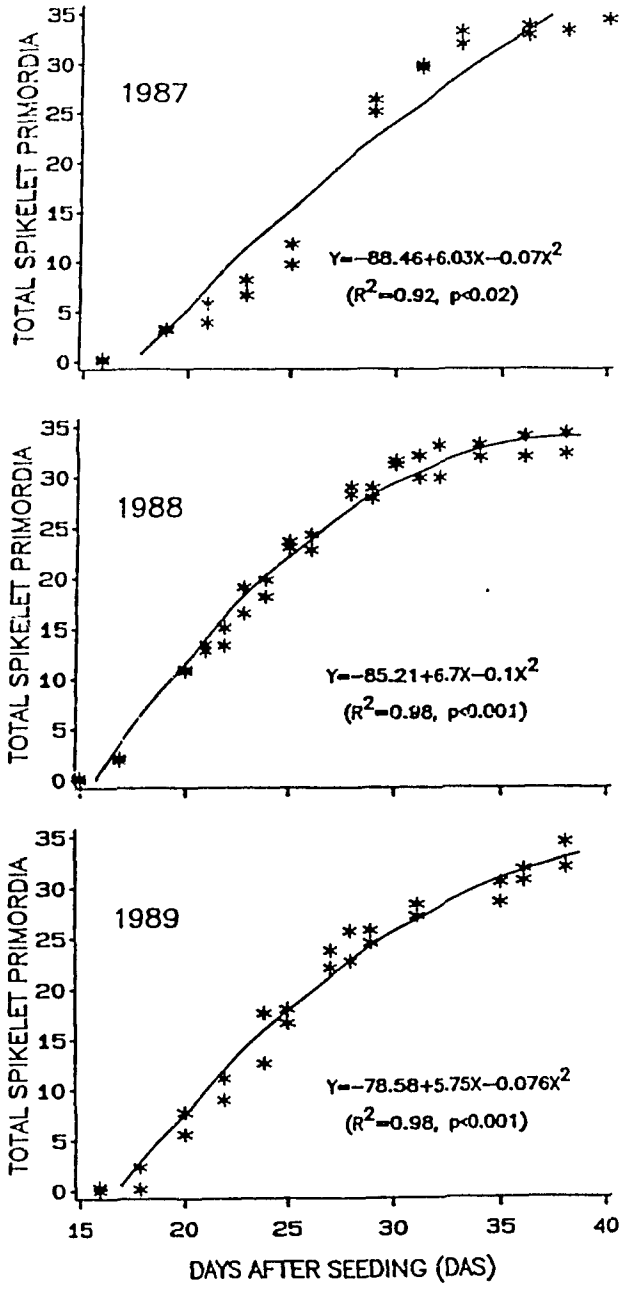

Fig. 3.1. Total primordia number as a function of days after seeding in each of 1987, 1988 and 1989. Each data point is a mean of at least 12 measurements except that the initial point is a mean of 5 plants. The model and the curve were based on the Data from 15 DAS to the date of maximum number of spikelet primordia (usually 38 to 40 DAS).

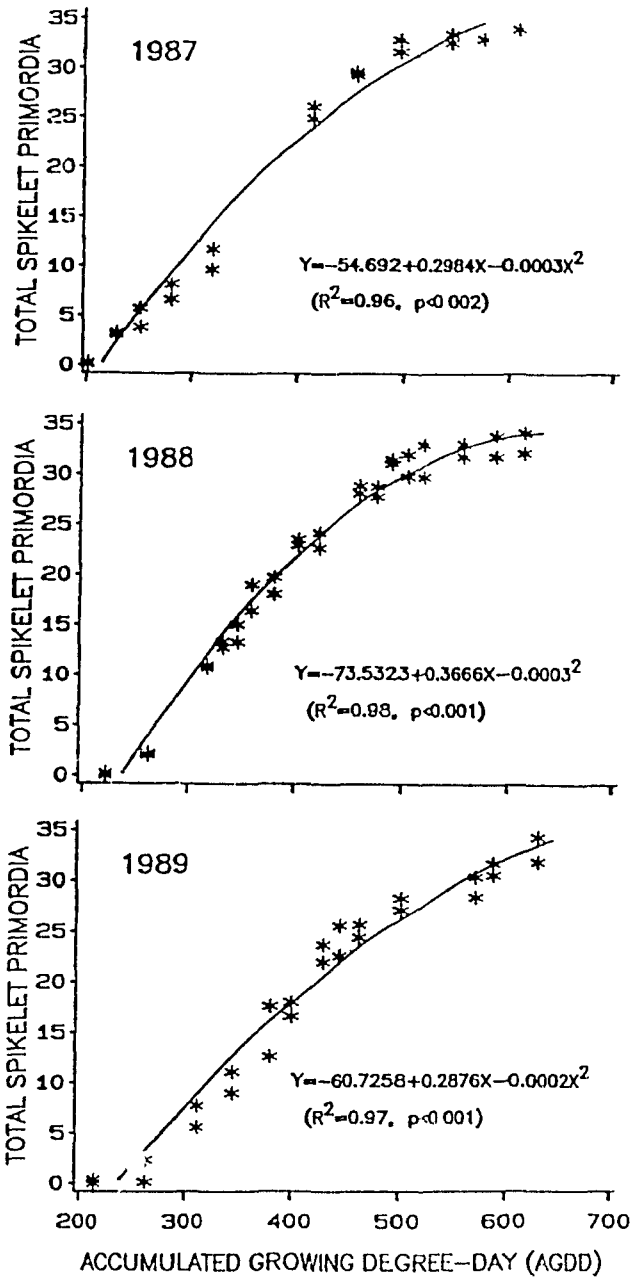

Fig. 3.2. Total primordia number as a function of accumulated growing-degree days (AGDD) in each of 1987, 1988 and 1989. Each data point is a mean of at least 12 measurements except that the initial point is a mean of 5 plants. Growing degree-day was accumulated from days after seeding. The model and the curve were based on the Data from 15 DAS to the date of maximum number of spikelet primordia (usually 38 to 40 DAS).

Preface to Section 4

Section 4 is the material contained in a manuscript by Ma and Smith (1991b) published in the Agronomy Journal (in press). The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table or figure is presented at the end of the section.

Following the description and discussion of the pattern and dynamics of barley main-stem apical development in Section 3, the influence of chlormequat or ethephon application timing on the main-stem apical development and tip spikelet abortions is addressed in this section.

Section 4

APICAL DEVELOPMENT OF SPRING BARLEY IN RELATION TO CHLORMEQUAT AND ETHEPHON

4.1 Abstract

There is considerable interest in the use of plant growth regulator(s) (PGR) to control lodging in spring barley (Hordeum vulgare L.), and to increase the number of spike-bearing tillers through early application. PGR application is likely to have effects on the development of reproductive structures in both main-stem and tiller apices. The objective of this study was to investigate the timing and dynamics of barley main-stem apical development as influenced by chlormequat chloride (2-chloroethyl trimethylammonium chloride; CCC) or ethephon (2-chloroethyl phosphonic acid) treatment. A 3-yr field study using widely grown cultivars, 'Leger' and 'Cadette', was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquept) at Emile A. Lods Agronomy Research Centre, McGill University, Canada, from 1987 to 1989. Treatments consisted of application with CCC and ethephon at Zadoks growth stages (ZGS) 13, 30 and 39. Data were collected on growth regulator induced plant changes in 1) external morphological characters, 2) apical development, and 3) spikelet primordium abortions. ZGS 13 application of CCC retarded development of the main-stem apex from shortly after application to awn elongation and reduced the number of aborted spikelet primordia. Unlike CCC, the retarding effect of ethephon on main-stem apical

development was not shown until a few days after its application (when the maximum number of main-stem primordia was reached), which may have promoted tiller survival. In general, the application of PGRs reduced the apical dominance of dominant sinks (main-stem apex and/or central spikelets of the rachis) allowing the survival and greater development of more subordinate sinks (tillers and/or distal rachis spikelets).

4.2 Introduction

The grain yield of barley (Hordeum vulgare L.) can be divided into several components - the number of spikes per plant or unit land area, grains per spike and weight per grain (Petr et al., 1988). These components are dependent on processes controlling apical development and grain fill. The apical development determines the number of grains per spike as well as the number of spike-bearing shoots, while grain fill influences grain size and plumpness through partitioning of photoassimilates among plant organs.

Numerous experiments have shown that plant growth regulators (PGR) shorten cereal stems and control lodging; however, their direct effects on the formation of yield components are less clear. Paterson et al. (1983) found that application of ethephon (2-chloroethyl phosphonic acid) was substantially less effective, and only 11 % of the treatments resulted in an economic increase in grain yield. Application of chlormequat (2-chloroethyl trimethylammonium chloride, CCC)and Terpal C (a 2:1 mixture of chlormequat and ethephon) on spring and winter barley resulted in an economic increase in grain yield in only 36 % and 20 % of treatments, respectively. Furthermore, a

statistically significant yield reduction due to chlormequat and ethephon was found in 16 % and 17 % of treatments, respectively. Brown and Earley (1973) showed that application of ethephon to oats (Avena sativa L.) resulted in a grain yield reduction. Green et al. (1988) reported that mepiquat chloride (1,1 - dimethyl - piperidinium chloride), which produces effects similar to chlormequat, had the potential to increase grain yield only under conditions of lodging. Causes of the widely varying responses to PGR applications are uncertain, and the physiological basis of PGR action is not fully understood.

From seedling establishment to the pre-heading stage, apical development and spike growth influence the production and survival of spikelets and grain number per spike. The processes of shoot apex differentiation have been investigated (Kirby and Appleyard, 1981). Many scales have been developed to describe apical development and morphogenesis (Aspinall and Paleg, 1963; Kirby and Appleyard 1981; Waddington et al., 1983). The stage of apical development at a certain period is generally expressed by the most advanced primordia in the apex (Kirby and Faris, 1970).

Environmental factors that affect shoot apical development in cereal crops include temperature (Halse and Weir, 1974), light (Rahman et al., 1977), water stress (Nicholls and May, 1963), and day length (Allison and Daynard, 1976). Investigations have also been conducted on field management factors such as plant population (Kirby and Faris, 1970) and sowing date (Wright and Hughes, 1987). Since growth regulators such as chlormequat and ethephon have the ability to reduce

the dominance of main-stem apices (Koranteng and Matthews, 1982), they should affect the rate and duration of cereal inflorescence formation and, subsequently, spikelet production and survival. The number of grains per spike might, therefore, be affected by the application of PGR. There have been recent investigations of hormonal manipulation of growth and developmental phenomena within the spike (Petr et al., 1988).

Unfortunately, however, few studies have addressed the effects of PGR on the processes of growth and development of the cereal inflorescence. The objective of this study was to investigate the processes of main-stem apical development of spring barley under continental climatic and field conditions, and to evaluate the effects of chlormequat and ethephon at normal rates (Thomas, 1982) on spikelet differentiation, growth and development, when applied at three physiological stages: beginning of tillering (Zadoks' growth stage [Zadoks et al., 1974] ZGS 13), onset of stem elongation (ZGS 30), or appearance of flag-leaf ligule (ZGS 39).

4.3 Materials and Methods

A 3-yr field study was conducted from 1987 to 1989 in a Bearbrook clay soil (fine, mixed nonacid, mesic Humaquept) at the Emile A. Lods Agronomy Research Centre, Macdonald College of McGill University, Canada. The previous crops were barley in 1987, alfalfa (Medicago sativa L.) in 1988 and oat in 1989. The land received a basal dressing of 300 kg ha^{-1} of 5-9-17 NPK commercial fertilizer, 100 kg N ha^{-1} as ammonium nitrate was applied immediately after seeding.

Seeding took place on 3 May in both 1987 and 1988, and on 1 May, 1989, at a rate of 450 seeds m^{-2}. Approximately 400 plants m^{-2} were established.

The experiment was a 2 by 3 by 2 factorial in 1987, and a 2 by 3 by 3 factorial in both 1988 and 1989, arranged in a randomized complete block design with 4 replicates. Two cultivars, 'Cadette' (a short-stature lodging resistant) and 'Leger' (a taller lodging susceptible), were treated with ethephon (480 g a.i. ha^{-1}), chlormequat (1200 g a.i.ha^{-1}), or received no PGR. Treatments were applied at ZGS 13 (third leaf fully expanded), ZGS 30 (the onset of stem elongation: not included in the 1987 experiment), or ZGS 39 (flag-leaf ligule just visible).

Plots were 4.4 m long at seeding with 22 rows spaced 10 cm apart. One half (11 rows) of each plot was used for taking samples for the investigation of apical development, and the remainder was used for yield determination (Section 6).

Assessment of apical development was based on the methods described by Aspinall and Paleg (1963) and Kirby and Appleyard (1981). At each sampling date, three consecutive representative plants were taken from one of the central rows for each of the treated and control plots. The row, and the section within the row from which the plants were harvested was randomly determined before each sampling. Plants were always selected so as to have a border of at least three adjacent spaced plants on either side within the row, and on either side in adjacent rows. No samples were taken from plot border rows. Sampling was conducted every 2 to 3 days over a period of 3 weeks, and started

approximately 15 days after seeding, which coincided with emergence of the second leaf. Early sampling allowed staging of main-stem apices when PGR were applied. The sampling interval was lengthened to every fourth or fifth day after the apex reached the awn initial stage.

To determine the stage of apical development of sampled plants, leaves were removed from the main stem to expose the apex. The stage of development of the main-stem apex of each plant was determined using a binocular microscope. For samples taken to determine development stage immediately prior to the first PGR application (ZGS 13) stage was assigned according to the development of the most advanced primordium. It may be more sensitive using a scale to describe the whole spike as large variations in the stages of development among primordia exist. The most advanced primordia of two spikes can be at the same stage, while the less developed primordia can be at different stages. A scale that indicated the average development stage of the whole spike was developed. Thus, following the first PGR application (ZGS 13), observations were taken on all plots using a weighted (over the whole embryonic-spike) apical stage. The weighted stage of apical development of each main-stem apex was determined according to the following formula:

$$S_w = \Sigma C_i Y_i \; / \; \Sigma C_i$$

Where S_w = weighted stage,

C_i = number of primordia in the i^{th} stage,

Y_i = the numerical value for the i^{th} stage according to Aspinall and Paleg (1963).

For example, if the main-stem apex of one plant is in Stage 7, i.e.

lemma initial visible, with five primordia at this stage, three primordia in Stage 6, five primordia in Stage 5, eight primordia in Stage 4 and two primordia in Stage 3. Then, S_w = 5.0. The apex of another plant from treated plot also may be in Stage 7 with two primordia at that stage, four primordia in Stage 6, four primordia in Stage 5, ten primordia in Stage 4, and three primordia in Stage 3. Then S_w=4.7. This provides a sensitive method for direct measures of the effects of treatments on apical development. In 1987, one replicate of the sampled plants was fixed and stored in a FAA solution (9:9:1:1 of ethanol:water:glacial acetic acid:formalin) for later verification.

Near the end of apex development, the primordia at the tip and the base of the embryonic-spike lost their glistening appearance, became duller and whiter, and were considered to be aborted (Kirby and Faris, 1970). The number of aborted spikelet primordia was measured at early heading stage (ZGS 51).

By ZGS 39 apical development was nearly completed, and there were no observable effects of PGR application on main-stem apical development or on spikelet abortion. Results reported in this paper include only observations from the earlier PGR applications (ZGS 13 and 30).

Rainfall and temperature data were collected at the meteorological station of the Emile A. Lods Agronomy Research Centre, not more than 500 m from the site used.

Statistical analysis was conducted according to the Statistical Analysis System (SAS Institue, 1985). An F-test (Steel and Torrie,

1980) was used to determine whether the variations caused by treatments and their interactions were significant. Within each cultivar the values of control plots for each time of PGR application were pooled, for an overall control mean. Differences among treatments were compared using a protected least significant difference (LSD) test at the 0.05 level of significance. For effects of PGR treatments on apical development tables included data from the first sampling date after each time of PGR sprayed, and thereafter for each data when the pattern of development differences changed among treatments. Data from sampling dates when the pattern of differences is the same as the preceding sampling date have been omitted.

4.4 Results and Discussion

Monthly rainfall for May, June, and July was 72, 116, and 105 mm in 1987, 47, 75, and 37 mm in 1988, and 84, 100 and 37 mm in 1989, respectively. The mean rainfall of these months for the last 15 yr was 84, 100, and 37 mm. Low precipitation in 1988 represented a dry summer. Daily maximum and minimum temperatures were plotted in Fig 4.1. Large variations for both temperatures and total monthly precipitation existed among years, which attributed to yearly variations on apical development. For example, growing conditions in 1988 were very different from those in 1987 and 1989, with a long period of low precipitation and high temperature occurring after seedling establishment. Under such moisture-stress conditions, the development of main-stem apices was accelerated.

Apical Development Stages at Zadoks Growth Stage 13

In 1987, there was no significant difference between cultivars for apical initiation stages 1 d prior to PGR application, although the apex was slightly more advanced in Leger than Cadette. The most advanced apices were at the double ridge stage.

In 1988, the stage of apical development was significantly different between cultivars one day prior to the first application of PGR. Plants of Cadette were between Stages 4 and 5 (spikelet primordia rapidly initiating), while those of Leger were between Stages 6 and 7 (lemma initials recognizable). Differences also existed between 1987 and 1988. For example, 1 d prior to the ZGS 13 PGR application, Leger was at the double ridge stage in 1987 and the lemma initial stage in 1988.

The early growing season of 1989 was atypically hot, which accelerated main-stem apical development. One day prior to the ZGS 13 PGR application the main-stem apices were at the triple mound stage for Cadette, and at the glume initial stage for Leger.

Apical development did not always keep pace with external growth stages such as ZGS. For instance, in 1987 at ZGS 13 the apices of both cultivars were approximately at the double ridge stage, while at this same ZGS they were more advanced in other seasons. Differences were also noted between cultivars. These observations agree with Cartwright et al. (1985), who claim that no relationship existed between apex stage and ZGS in the early stages of plant development. This phenomenon could partially explain the yield variations observed

in different experiments or in different years even though PGR are applied at the same ZGS. The components of grain yield form at different growth stages and different apex developmental stages. The sensitivity to external stimulation should differ if the plants are in different apical developmental stages. Therefore, it might be more reliable to test the effects of PGR based on the stage of apical development.

Plant Growth Regulators on Apical Development

In 1987, significant differences were found among treatments, following PGR application at ZGS 13, although the response varied between cultivars (Table 4.1). In Cadette, application of both ethephon and chlormequat at ZGS 13 significantly decreased weighted stage means of apical development. The retarding effect of chlormequat lasted about 16 days, after which the apparent differences disappeared. The effect of ethephon on the apex differentiation lasted for less time, being significant at 2 d after the first application of PGR, but there was no observable effect thereafter. In Leger neither chlormequat nor ethephon applied at ZGS 13 had an observable effect on weighted stage means of main-stem apex development immediately after application. Starting from flag leaf emergence (ZGS 37) to heading, both chlormequat and ethephon treatments significantly retarded main-stem apical development in Leger, but had no effect in Cadette (Table 4.1).

The effects of growth regulator on the weighted stage means of apical development for 1988 are presented in Table 4.2. For both

cultivars early chlormequat application (ZGS 13) slowed apex differentiation. The effect did not last as long for Leger as for Cadette, and Leger was less affected by both chlormequat and ethephon. As spikelet differentiation was almost completed by ZGS 30, it is not surprising that PGR did not affect the timing of apical development when applied at either ZGS 30 or 39.

The summer of 1989 was relatively mild, and the climatic conditions were comparable to those of 1987, except for July when much less rainfall was received. Nonetheless, the effects of PGR on the weighted stage means of apical development (Table 4.3) were similar in both seasons, with the exception that application of chlormequat at ZGS 13 in 1989 also showed a consistent retardation effect on main-stem apical development in both cultivars, and Cadette did not show 1987 response to ethephon. Early application of ethephon, at ZGS 13 also significantly retarded the apical development of Leger as shown by plants sampled at ZGS 13 + 7 d and + 9 d.

The results reported here indicate that the apical development of spring barley was retarded by the application of chlormequat at ZGS 13, in most cases, and at ZGS 30 in some sampling data. The effect of ethephon, applied at ZGS 13, on apical development depended upon environmental conditions. The results showed that cultivars may respond to PGR in different ways. For Cadette, for example, both chlormequat and ethephon significantly retarded main-stem apical development when applied at ZGS 13, while for Leger, a significant retarding effect by early ethephon treatment was found at a few days later following the application (Tables 4.1, 4.2 & 4.3). Similar

effects with application of mepiquat chloride were reported in England (Waddington and Cartwright, 1988). Waddington and Cartwright (1988) demonstrated that application of mepiquat chloride at the lemma stage retarded the development and growth of spring barley main-stem spike. The inhibition effects of the PGR on main-stem apical development - reducing apical dominance - at early growth stage may help tiller production, since more assimilates may be available for tiller initiation and growth. This explained the observations of vigorous roots (Koinov and Radnev, 1981) and greater tiller number (Koranteng and Matthews, 1982).

Plant Growth Regulators on Spikelet Primordia Abortion

Shortly after ZGS 39, changes were noted in the primordia at the tip and the base of the spikes. In 1987, treatments resulted in differences in the number of aborted spikelet primordia. There were significant interactions between PGR treatment and cultivar, and PGR treatment and time of application. Both ethephon and chlormequat significantly reduced the number of aborted spikelet primordia by 0.7 to 1.6 in Leger, but had no effect in Cadette (data not shown). Early application (ZGS 13) of chlormequat significantly decreased the number of aborted spikelet primordia by 2.5 compared to control plants, while late application of chlormequat or ethephon showed no significant effect (Table 4.4).

The main effect of PGR on primordia abortion in 1988 was similar to that of 1987 (data not shown). Both chlormequat and ethephon

significantly reduced the number of aborted primordia per main-stem embryonic-spike by 1.6 to 2.7 in 1988 (Table 4.4). There was, however, no significant interaction either between cultivar and PGR treatment, or PGR treatment and time of application on the number of aborted spikelet primordia (Table 4.4).

The 1989 data on the abortion of spikelet primordia are presented in Table 4.4. A significant time of application by PGR treatment interaction was also found, though there was no cultivar by PGR treatment interaction. Similarly to 1987, early application (ZGS 13) of chlormequat significantly reduced the number of aborted spikelet primordia. Furthermore, application of ethephon at ZGS 30 showed significantly fewer aborted spikelet primordia.

Baker and Gallagher (1983) showed evidence suggesting that for wheat the number of spikelets that develop in field-grown plants is established at the double ridge stage. They suggest that effects on the number of grains per spike after this stage are mainly due to alteration in grain set per spikelet. In the case of barley, which has a different inflorescence structure from wheat, our evidence suggests that application of PGR after the double ridge stage may increase the number of grains per spike by reducing the number of spikelet primordia that eventually abort (Table 4.4).

In conclusion: (i) an early application of chlormequat at ZGS 13 significantly delayed the development of the main-stem apices of spring barley, (ii) the number of aborted spikelet primordia was significantly reduced by ZGS 13 chlormequat treatment, probably

because that differences in rate of development among the spikelets within a spike was minimized, (iii) unlike chlormequat, during the earlier growth stages, ethephon did not show immediately retarding effect on the main-stem apex, (iv) however, the retarding effect of ethephon was obvious a few days after the application, and (v) apical development was not linked with external morphological development (eg. ZGS), which might explain variations in grain yield following application of PGR.

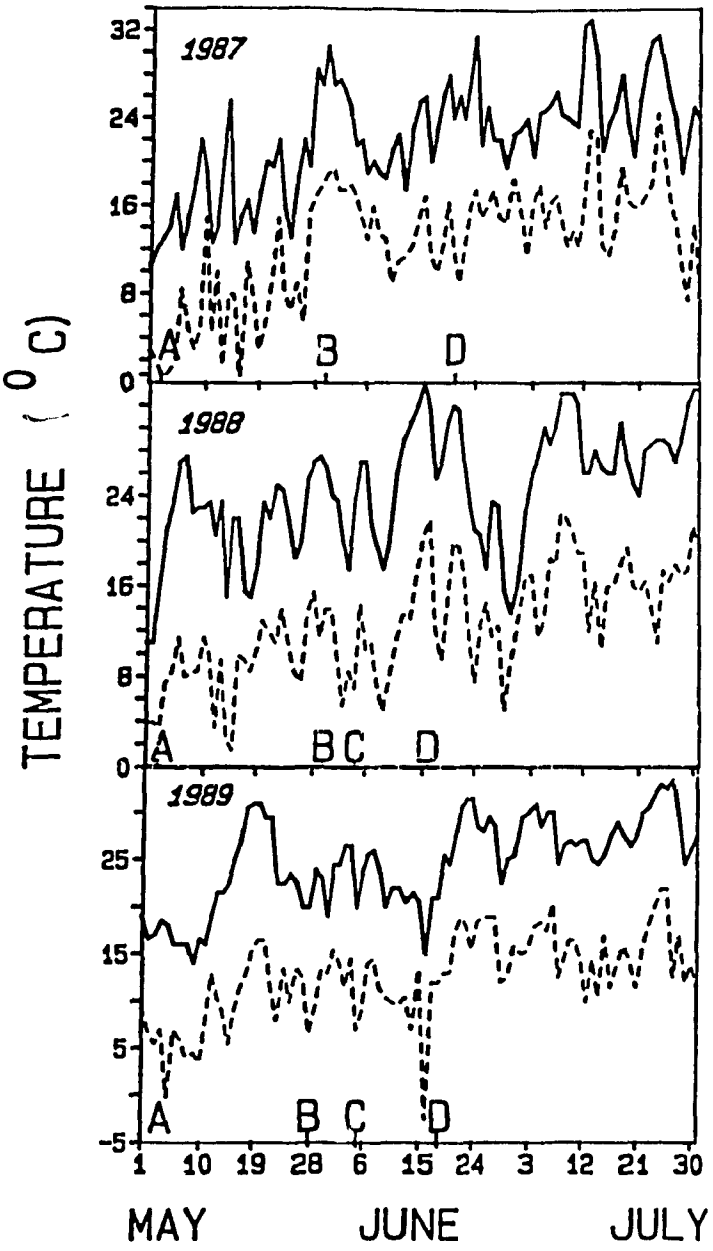

Fig. 4.1. Growing season daily maximum and minimum temperature (^{0}C) for 1987, 1988, and 1989. A, date of seeding; B, C, and D, represent dates of application of plant grow regulators (PGR) at Zadoks growth stage (ZGS) 13, 30, and 39, respectively. Solid line represents maximum temperature; broken line represents minimum temperature.

Table 4.1. Weighted stage means of main-stem apical development as affected by Zadoks growth regulator (ZGS) 13 application of plant growth regulator (PGR) within cultivar at selected sampling dates in 1987.

Treatment	Days after ZGS 13			
	2	4	16	24
		Cadette		
Control	5.9† a	7.2 a	9.6 b	10.0 c
Ethephon	4.8 b	7.0 a	9.7 b	10.0 c
Chlormequat	4.3 b	5.6 b	9.4 c	10.0 c
		Leger		
Control	5.7 a	7.6 a	9.9 a	10.6 a
Ethephon	5.8 a	7.4 a	9.6 b	10.1 bc
Chlormequat	5.8 a	7.2 a	9.7 b	10.2 b
Cultivar * PGR	**	*	*	*

*, ** Significant at 0.05, 0.01 levels of probability, respectively.

† Means of the same cultivar within the same column followed by different letter are significantly different by a protected LSD ($P < 0.05$) analysis.

Table 4.2. Weighted stage means of main-stem apical development as affected by treatment combinations at selected sampling dates in 1988.

Treatment	ZGS† Stage	Days after ZGS 13 2	8	16	20
			Cadette		
Control		6.8‡ c	9.4 a	9.9 a	10.5 a
Ethephon	13	6.8 c	9.5 a	9.7 b	10.5 a
Ethephon	30§	-	9.4 a	9.7 b	10.5 a
Chlormequat	13	6.3 d	9.0 b	9.9 a	10.6 a
Chlormequat	30	-	9.0 b	9.6 b	10.6 a
			Leger		
Control		7.5 a	9.3 a	10.0 a	10.7 a
Ethephon	13	7.2 ab	9.4 a	10.0 a	10.7 a
Ethephon	30	-	9.4 a	10.0 a	10.7 a
Chlormequat	13	6.9 bc	9.4 a	10.0 a	10.6 a
Chlormequat	30	-	9.4 a	9.9 a	10.7 a
PGR X ZGS		*	**	*	NS

NS Not significant at the 0.05 level of probability.

*, ** Significant at 0.05, 0.01 levels of probability, respectively.

† ZGS = Zadoks growth stage.

‡ Means of the same cultivar within the same column followed by different letter are significantly differen. by a protected LSD ($P < 0.05$) analysis.

§ PGR at ZGS 30 was applied 5 days after ZGS 13 application.

Table 4.3. Weighted stage means of main-stem apical development as affected by treatment combinations at selected sampling dates in 1989.

Treatment	ZGS† Stage	Days after ZGS 13				
		2	7	9	13	25
				Cadette		
Control		6.6‡a	9.1 a	9.5 a	9.6 a	11.0 a
Ethephon	13	6.4 a	8.4 c	9.4 a	9.5 a	11.0 a
	30‡	-	8.9 b	9.4 a	9.6 a	11.0 a
Chlormequat	13	5.7 b	8.9 b	9.1 b	9.6 a	11.0 a
	30	-	8.2 d	9.1 b	9.5 a	11.0 a
				Leger		
Control		6.2 a	8.8 b	9.4 a	9.6 a	11.0 a
Ethephon	13	6.2 a	8.1 d	8.5 b	9.5 ab	10.9 b
Ethephon	30	-	8.5 c	9.1 b	9.5 ab	10.4 c
Chlormequat	13	5.6 b	8.4 c	8.6 c	9.4 b	11.0 a
Chlormequat	30	-	8.2 d	9.0 b	9.5 ab	11.0 a
Cultivar * PGR		*	**	*	**	**

*, ** Significant at 0.05, 0.01 levels of probability, respectively.

† ZGS = Zadoks growth stage.

‡ Means of the same cultivar within the same column followed by different letter are significantly different by a protected LSD ($P < 0.05$) analysis.

‡ PGR at ZGS 30 was applied 8 days after ZGS 13 application.

Table 4.4. Mean number of aborted spikelet primordia as affected by time of application within PGR treatment.

Treatment	ZGS† Stage	1987	1988	1989
Control		15.3 ab‡	14.9 a	12.0 ab
Ethephon	13	14.8 b	13.3 ab	10.3 bc
Ethephon	30‡	-	12.2 b	9.3 c
Chlormequat	13	12.8 c	12.7 b	9.2 c
Chlormequat	30	-	12.3 b	9.7 bc
PGR x ZGS		NA	NS	*

NA Not appliable.

NS Not significant at 0.05 level of probability.

*, ** Significant at 0.05 level of probability.

† ZGS = Zadoks growth stage.

‡ Means within the same column followed by different letter are significantly different by a protected LSD ($P < 0.05$) analysis.

‡ PGR at ZGS 30 was applied 5 and 8 days in 1988 and 1989, respectively, after ZGS 13 application.

Preface to Section 5

Section 5 is the material contained in a manuscript by Ma and Smith (1991c) submitted to the Agronomy Journal. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table is presented at the end of the section.

Following discussion of spring barley apical development as affected by CCC or ethephon application timing in Section 4 the effects of PGR treatment on tillering pattern and dynamics of field barley are discussed in this section.

Section 5

MODIFICATION OF TILLERING DYNAMICS IN SPRING BARLEY BY APPLICATION OF CHLORMEQUAT OR ETHEPHON

5.1 Abstract

Application of plant growth regulator(s) (PGR) to control lodging in cereal crops often increases the number of tillers and/or spikes. It is not clear whether the increment in spike numbers is due to enhanced tiller production or to improved tiller survival. The objective of this study was to evaluate the effects of chlormequat (CCC) and ethephon timing on tiller production and subsequent tiller growth and development in spring barley (Hordeum vulgare L.). A 3-yr field study using the widely grown cultivars, 'Leger' and 'Cadette', was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquept) at the Emile A. Lods Agronomy Research Center, McGill University, Canada, from 1988 to 1990. Treatments consisted of application of CCC (1.2 kg a.i. ha^{-1}) and ethephon (0.48 kg a.i. ha^{-1}) at Zadoks growth stages (ZGS) 13, 30 and 39. Tiller dynamics were monitored at ZGS 12, ZGS 32, ZGS 51, and ZGS 90. The results demonstrated that plants treated with an early application of CCC at ZGS 13 or ethephon at ZGS 30 produced greater numbers of shoots, which appeared later in time, than control plants. Number of spike-bearing shoots was increased by early PGR treatment, primarily by enhancement of tiller number rather than tiller survival. Late application of CCC (ZGS 39) or application of ethephon at ZGS 39 when most of the tillers had emerged resulted in a higher number of spike-bearing shoots, mostly through increased tiller

survival.

5. 2 Introduction

Spring barley (Hordeum vulgare L.) is the major small grain crop produced in Quebec, Canada. It is usually produced using moderate nitrogen fertilizer applications (60 to 90 kg ha^{-1}). Since the 1960's, European cereal producers have been using more intensive management strategies, involving increased N fertilizer use and fungicides. High N fertility promotes lodging in cereals, but the use of plant growth regulator(s) (PGR) as antilodging agents can reduce lodging and aid in maintaining yield potential (Green 1986; Dahnous et al. 1982). Among synthetic PGR chlormequat (2-chloroethyl trimethylammonium chloride, CCC) and ethephon (2-chloroethyl phosphonic acid) are the most used in agricultural production. Both PGR have the ability to shorten or stiffen cereal culms, thereby reducing lodging losses in conventional tall lodging-susceptible cultivars particularly under conditions of high fertility and favorable precipitation. Some recent studies have demonstrated that early application of these PGR can enhance grain yield through increasing the number of spike-bearing shoots per unit land area without affecting plant height or lodging (Waddington and Cartwright, 1986; Koranteng and Matthews, 1982; Cartwright and Waddington, 1981; Matthews et al., 1981).

CCC is an anti-gibberillin agent. Its action is through inhibition of cyclization of trans-geranyl-geranyl-pyrophosphate, which leads to a low concentration of kaurene (a GA_3 precursor), and

therefore, reduced levels of endogenous gibberellins (Jung, 1984). Although CCC has been shown to be less successful in reducing height and lodging in barley, due to poor absorption and rapid transport within the barley plant (Skopik and Cervinka, 1967), its potential in the manipulation of tiller growth and development stimulated the investigation of its potential use in spring barley. In addition, Alcock et al. (1966) found that ^{11}C-labeled CCC moved more slowly in barley than in wheat, opposite to the findings of Skopik and Cervinka (1967). In any case CCC may reduce apical dominance of barley main shoots leading to more within-plant uniformity, more tillers per plant, or per unit area and a greater number of spike-bearing tillers (Waddington and Cartwright, 1986; Matthews et al., 1981; Bokhari and Youngker, 1971). Ethephon is a synthetic growth regulator that releases ethylene slowly inside plant tissues through a pH-dependent reaction (Warner and Leopold, 1969). The availability of ethephon has greatly increased the use of ethylene in agronomic and horticultural production. Ethylene inhibits the movement of auxin in stem tissues and auxin biosynthesis (Evan, 1984), thereby reducing auxin's ability to promote stem elongation and to inhibit tiller bud outgrowth (Woodward and Marshall, 1987). Many studies have shown that ethephon can prevent plant lodging in a wide range of plant species (Dahnous et al., 1982) via an inhibition of stem elongation (Sachs and Hachett, 1972), leading to reduced plant height.

For lodging control, the recommended development stages for PGR application are from Zadoks' (Zadoks et al., 1974) growth stages (ZGS) 30 to 31 for CCC and ZGS 37 to 45 for ethephon (Caldwell et al., 1988;

Thomas, 1982). Previous studies on the effects of earlier CCC application to increase grain yield by altering yield components were carried out under cool, long growing season conditions in Europe (Waddington and Cartwright, 1986; Koranteng and Matthews, 1982; Cartwright and Waddington, 1981; Matthews et al., 1981). It is generally felt that environmental changes have a significant impact on tiller production and survival in cereals (Lauer and Simmons, 1989). In a previous paper, we found that early application of either chlormequat or ethephon retarded the development of main-culm apices of spring barley (Section 4), evidence indicated that such inhibition of main culms by the PGR could release tillers from the suppression of apical dominance, thereby increasing tiller production and the number of spike-bearing tillers. Application of ethephon during the period of ZGS 37 to ZGS 45 increased spike number, mostly by enhancing tiller survival, since most of the tillers had emerged at this time (Simmons et al., 1988). Early application of ethephon has been demonstrated to increase the number of spike-bearing tillers (Section 7). Matthews et al. (1981) found that CCC increased the survival probability of secondary barley tillers by hastening their appearance and increasing their size. Woodward and Marshall (1988) demonstrated that tiller bud initiation and subsequent growth were significantly increased by ethephon treatment, and suggested that by its effect on auxin availability ethephon increased the ratio of cytokinin to auxin, thereby promoting tiller bud outgrowth. Reports of PGR effects on tiller growth dynamics and development under intensively managed field conditions are rare. Whether PGR treatment increased tiller number

or caused a larger proportion of tillers to progress to the spike production stage or a combination of the two, is not clear. The objectives of this study were to (i) ascertain the direct effect of CCC (1.2 kg ha^{-1}) and ethephon (0.48 kg ha^{-1}) on tiller production and (ii) clarify whether the observed increase in spikes per unit land area following PGR treatment resulted from more tiller production or greater tiller survival and development. In this work the PGR was applied at three physiological stages: the beginning of tillering (ZGS 13), the onset of stem elongation (ZGS 30), or the appearance of flag-leaf ligule (ZGS 39), under continental climatic field conditions.

5.3 Materials and Methods

A 3-yr study on the effects of CCC and ethephon timing of application to spring barley cultivars was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquat) at the E. A. Lods Agronomy Research Center, Macdonald College of McGill University, Quebec, Canada. Meteorological data, field management and experimental design for 1988 and 1989 have been reported previously (Section 4).

Briefly, the climatic conditions were more or less normal in 1989 and 1990, while warmer and dryer in 1988, compared to the 15-yr averages (Ma and Smith, 1991b). The preceding crops were alfalfa (Medicago sativa L.) in 1988, oat in 1989, and barley in 1990. In each case, the land received a basal dressing of 300 kg ha^{-1} of 5-9-17 NPK commercial fertilizer prior to seeding. Thirty kg ha^{-1} in 1988 and 100 kg ha^{-1} in the other seasons, respectively of ammonium nitrate N were broadcast onto the plots immediately after seeding. Each plot

was 4.2 m long at seeding and consisted of 22 rows at a 10 cm spacing. Prior to harvest these were trimmed back to 3.4 m to eliminate edge effects along the sides of the pathways between blocks. Certified seed treated with Vitaflo 280 (carbathiin and thiram) was planted at approximately 450 seeds m^{-2}, using a tractor-drawn Kincaid cone-type plot seeder on May 3, 1988; May 1, 1989 and 1990. In each year the seeding density ranged from 400 to 450 plants m^{-2}. For weed control a mixture of 280 g a.i. ha^{-1} bromoxynil (3,5 - dibromo -4-hychroxybenzonitrile, Pardner) and 646 g a.i. ha^{-1} diclofop-methyl [methyl 2 - (4 - (2,4 - dichlorophenoxy) phenoxy) propanoate, Hoe-grass] was applied at Zadoks' growth stage (ZGS) 12.

Application of CCC or ethephon was made with a sprayer mounted on a lawn tractor in 1988, and by means of a backpack sprayer in 1989 and 1990. In all cases application was through a boom fitted with four Tee-jet 8002 flat fan nozzles, and with a spray width of 1.1 m. The spray volume was 345 L ha^{-1}, at a pressure of 207 kPa. Citowett Plus at 0.05 % (v/v) was used as a surfactant. During spraying, the target plot was surrounded by a portable plastic barrier to prevent PGR drift into adjacent plots.

Shortly after seedling emergence a 1-meter section in the third row. starting 50 cm at one end of each plot was marked for investigation of tillering dynamics. In 1988, only stand counts and final spike number were measured in the previously marked meter row. In 1989 and 1990, on 4 occasions, during seedling (ZGS 12), stem elongation (ZGS 32), heading (ZGS 51) and ripening (ZGS 90) stages the number of shoots (tillers plus main stems) in the meter row section

was determined for each plot. Earlier research has shown that ZGS 32 approximates the time of maximum shoot number of spring cereals (Simmons et al., 1982). It was expected that in barley application of CCC or ethephon would promote tiller production even after stem elongation. The maximum number of shoots should therefore appear after ZGS 32, approximately at the beginning of heading for PGR applied at ZGS 30. Since an uneven distribution of seeds is unavoidable there were variations of stand counts in the meter row. The shoot density was determined on the premarked meter row. This was expressed in a m^{-2} basis after covariate adjustment for plant density.

Data were analyzed with the SAS system (SAS Institute, 1985). For each measurement, experimental error variances from each year were tested for homogeneity using Bartlett's test (Gomez and Gomez, 1984). Combined analysis of variance across years was performed and reported if the error variances were homogeneous. The F-test (Steel and Torrie, 1980) was used to determine whether the variations caused by treatments and their interactions were significant. Probabilities of less than or equal to 0.05 were considered significant for main effects and interactions. An F-protected least significant difference ($LSD_{0.05}$) was calculated to compare means of variables found to vary significantly. Within each cultivar the values of control plots for each application stage were pooled, for an overall control mean.

5.4 Results

Error mean square for each variable (number of shoots measured at different stages) across years was not always homogenous as tested by Bartlett's analysis. Yearly variation and the year by PGR interaction were both large. As indicated by the analysis of covariance plant density (number of plants m^{-2} measured at ZGS 12) was a significant covariable for shoots and spike-bearing shoots m^{-2} measured at all stages in 1989 and 1990, while this covariable was not significant for spike-bearing shoots in 1988 (data not shown). In order to compare treatment effects by a common criterion means of shoots m^{-2} adjusted for plant density are reported in all cases each year. Overall, application of CCC or ethephon tremendously influenced the number of shoots m^{-2}. Significant interactions of cultivar by PGR treatment, and PGR by application stage were found in most cases for each year of this 3-year study. For these reasons the treatment effects are discussed each year, in terms of PGR by cultivar and PGR by application stage even though as shown in the corresponding table those interactions were not always significant ($P \leq 0.05$) while the model and main effects were significant.

1988

In 1988, genotypic differences in spike-bearing shoots m^{-2}, as affected by PGR treatment, were highly significant. In general, Cadette, a semi-dwarf cultivar, had a significantly higher number of spike-bearing shoots m^{-2} than Leger, a standard tall cultivar. Application of ethephon increased the number of spike-bearing shoots

m^{-2} in Leger but not in Cadette (Table 5.1). It was observed that barley plants treated with ethephon at ZGS 39 or CCC at ZGS 30 produced a significantly larger number of spike-bearing shoots m^{-2} than the control plants or those that received PGR application at other stages (Table 5.2). On average, the control treatment had 1.32 spikes per plant while ethephon applied at ZGS 39 and CCC at ZGS 30 resulted in 1.50, and 1.57 spikes per plant, respectively, which represented a 13 to 19 % increment in spike-bearing shoots.

1989

In 1989, precipitation was high during the early barley development stages (Section 3), which facilitated tiller production. The analysis of variance for shoots m^{-2} at stem elongation (ZGS 32) and at heading (ZGS 51) showed an absence of cultivar x PGR interaction, indicating that the PGR were equally effective in both cultivars. Ethephon treatment resulted in more tillers than the control. A cultivar by PGR interaction occurred at plant maturity (ZGS 90); for Cadette ethephon treatment produced a larger number of spike-bearing shoots m^{-2}, while for Leger CCC treatment significantly increased this variable. In both cases the result was an increase of approximately 10 % over the control (Table 5.3). Application stage had a different effect for each PGR. When measured soon after the onset of stem elongation (ZGS 32) and only 3 d after PGR application, it was found that early application of ethephon (ZGS 13) dramatically increased the number of shoots m^{-2} while a ZGS 30 application of ethephon reduced this variable. At heading, however, a substantially higher number of

shoots m^{-2} was found to result from the ZGS 30 ethephon treatment. By maturity ethephon applied at both ZGS 13 and ZGS 30 produced a significantly higher number of spike-bearing shoots m^{-2}. Ethephon application at ZGS 39 decreased the number of spike-bearing shoots m^{-2}. Application of CCC produced the similar results in 1989. At stem elongation, CCC applied at ZGS 13 or ZGS 30 resulted in significantly higher number of shoots m^{-2} compared to those of control plots. However, significant differences in the number of spike-bearing shoots m^{-2} between CCC and control treatments were absent at heading (ZGS 51) but reappeared at maturity. Thus, as a result of enhanced tiller production, early application of CCC at ZGS 13 or ethephon at ZGS 30 barley plants produced 13 to 17 % more spike-bearing shoots m^{-2} than those receiving the control treatment (Table 5.4).

1990

In 1990, the cultivar by PGR treatment and PGR treatment by application stage interactions were significant in some cases. For Cadette ethephon treatment produced more shoots or spike-bearing shoots m^{-2} at all stages measured while no difference was found between control and CCC treatment. In contrast, application of either ethephon or CCC resulted in significantly more shoots and spike-bearing shoots m^{-2} by Leger (Table 5.5). Early application of ethephon (ZGS 13) significantly increased tillering. Ethephon applied at ZGS 30 had not altered the tiller production by ZGS 32. With ethephon applied at ZGS 13 or ZGS 30, dramatically higher numbers of shoots m^{-2} occurred at heading while significantly lower numbers of shoots m^{-2}

were found when ethephon was applied at ZGS 39. However, application of ethephon at ZGS 39 produced a larger number of spike-bearing shoots m^{-2} at maturity, which was attributable to an improved tiller survival. Early ethephon application (ZGS 13) decreased tiller survival. As a result, ethephon applied at ZGS 30 resulted in significantly higher number of spike-bearing shoots m^{-2} mainly through increased tiller production. In 1990, the plots assigned for CCC treatment had a slightly, although not significantly ($P>0.2$), higher plant density (number of plants m^{-2}) compared to those of control plots. Nonetheless, after adjusted for plant density CCC treatment did not significantly ($P>0.10$) increase the number of shoots or spike-bearing shoots m^{-2} at any stage of investigation (Table 5.6). A slightly, but not significantly ($P>0.10$), higher number of spike-bearing shoots m^{-2} was produced by CCC treatment at ZGS 30 or ZGS 39, which accounted for the significantly higher number of spike-bearing shoots m^{-2} in Leger (Table 5.5).

5.5 Discussion

Previous studies on the early application of CCC to winter or spring barley (before ZGS 30) did not show genotypic differences (Koranteng and Matthews, 1982; Williams et al., 1982; Matthews et al., 1981). With timely application of ethephon (ZGS 37 to 39) for lodging control Caldwell et al. (1988) demonstrated that different cultivars had different sensitivities to PGR treatment in terms of grain production and plant characteristics (reduced height and lodging). The results presented here showed that for tiller production Leger, the standard

tall cultivar, was more responsive to the early CCC or ethephon treatment than was Cadette, a semi-dwarf cultivar (Tables 5.1 and 5.5).

In spring barley tiller bud outgrowth, the total tillers and spike-bearing shoots per plant were all promoted by seed treatment with Terpal (a mixture of mepiquat chloride and ethephon), which inhibits gibberellin biosynthesis in a fashion similar to CCC (Caldwell et al., 1988), or in a similar manner to ethephon to interfere with auxin transport and biosynthesis (Evan, 1984), and induction of tillering can be explained by either mechanism (Woodward and Marshall, 1987). Early foliar application of CCC was shown to increase spike-bearing shoots per plant or per unit land area, probably due to enhanced tiller survival (Waddington and Cartwright, 1986; Cartwright and Waddington, 1981; Matthews et al., 1981). In this study, we found early application of ethephon at ZGS 30 (Tables 5.4 & 5.6) or CCC at ZGS 13 (Table 5.4) increased the number of shoots m^{-2} during the tillering phase. As a result, a larger number of spike-bearing shoots m^{-2}, obviously resulting from an enhancement of tiller production rather than tiller survival (Table 5.4), were produced with more or less the same survival rate (spike number / maximum shoot number). As early application of growth retardant has a transient suppression on the growth and development of main shoots, it is probable that more assimilates are available for tiller bud initiation and their subsequent growth and development. Cartwright and Jaddoa (1985) concluded that a tiller must reach a critical developmental stage before main-culm heading if it is to survive and

produce grain. Matthews et al. (1981) demonstrated that CCC treatment induced tillers to occur earlier. Early application of PGR probably promoted earlier tiller initiation and a higher maximum tiller number. Thus more tillers were produced but the proportion of spike-bearing tillers (determined by their size at plant heading) over the maximum tiller number was similar to control plants, in which a smaller number of tillers was produced. Naylor et al. (1987) reviewed literature illustrating that CCC applied before ZGS 30 appears to reduce the sink capacity of the main stems, thereby freeing assimilates to contribute to the growth of other parts of the plant, such as roots and tillers. This implies that more tillers would be produced by PGR treated plants since the dominance of the main-stem was reduced by the treatments. Late application of CCC (ZGS 39) or timely application of ethephon (ZGS 39) improved spike-bearing shoots by increasing the proportion of already existing tillers that produced productive spikes, that is, tiller survival, which confirmed the findings of Simmons et al. (1988). Ethephon applied to the crop at ZGS 39 was added for lodging control; by ZGS 39 most of the tillers had already emerged and modification of spike numbers was largely by enhancing tiller survival.

Matthews et al. (1981) reported that early CCC application induced tillering to occur earlier; approximately 2 wk after CCC treatment tiller numbers were increased although there was no difference between the CCC treatment and the control at crop maturity. In our study the maximum number of tillers per plant or unit land area usually occurred at ZGS 32 (Table 5.3) as Simmons et al. (1982)

reported. With application of PGR, however, this maximum appeared later, at approximately ZGS 45 to ZGS 51 (heading period) (Tables 5.4 and 5.6). There was a lag phase between PGR application stage and the effect of PGR on tillering. The normal stage for measuring the maximum tiller number (ZGS 32) was 2 to 3 d after PGR treatment, at ZGS 30, and did not reflect the ZGS 30 PGR effect. In a growth cabinet experiment, Woodward and Marshall (1988) observed that increased tiller emergence was detectable only 5 d after treatment and 20 % more tillers were produced by Terpal or ethephon application than by the control treatment at 15 d after application. There seemed to be a transition period for the plant response to these PGR, probably due to the following (i) absorption of PGR through leaf or stem tissues; (ii) transport of PGR inside the plant and to the apices, (iii) inhibition of the main stem initiation and growth, thus making more assimilates available for, or less inhibiting photohormone produced and/or moved to the tiller bud initials; (iv) tiller bud growth initiation; (v) tiller bud outgrowth and emergence. This whole process may take 5 d under controlled growth conditions (Woodward and Marshall, 1988) or longer under field conditions.

It should be noted that growing seasons for spring barley in Quebec are much shorter than those under which earlier European studies were conducted (Waddington and Cartwright, 1986; Koranteng and Matthews, 1982; Matthews et al., 1981). Under Quebec climatic and cultural conditions we found much less tillering had taken place, which contributed less to grain yield compared to main stems, particularly with hot and dry climatic conditions (Section 7). For

instance, 2 to 3 spike-bearing shoots per plant were normally produced in European spring barley when produced under high plant densities while under intensive management in Quebec spring barley plants produced only 1 to 1.5 spikes per plant, even with the application of PGR.

Table 5.1. Means of stand counts or least square means of shoots m^{-2} as affected by plant growth regulator (PGR) treatment within cultivar in 1988

PGR treatment	Plant stage at investigation	
	ZGS† 12	ZGS 90
	Cadette	
Control	316	493‡a
Ethephon	363	517 a
Chlormequat	327	512 a
	Leger	
Control	376	406 b
Ethephon	348	495 a
Chlormequat	393	464 ab
Cultivar x PGR	NS	*

† ZGS = Zadoks growth stage.

‡ Means in the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

* Significant at $P \leq 0.05$.

Table 5.2. Means of stand counts or least square means of shoots m^{-2} as affected by plant growth regulator (PGR) by application stage (ZGS) in 1988

PGR treatment	Application stage (ZGS)	Plant stage at investigation: ZGS 12	Plant stage at investigation: ZGS 90
		No. m^{-2}	
Control		348	452† c
Ethephon	13	340	465 bc
Ethephon	30	354	485 bc
Ethephon	39	375	569 a
Chlormequat	13	366	459 c
Chlormequat	30	352	536 ab
Chlormequat	39	358	468 bc
PGR X ZGS		NS	**

† Means in the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

Table 5.3. Means of stand counts or least square means of shoots m^{-2} at different stages of investigation as affected by PGR treatment within cultivar in 1989

PGR treatment	Plant stage at investigation			
	ZGS 12	ZGS 32	ZGS 51	ZGS 90
	No. m^{-2}			
		Cadett		
Control	443	703 c	544 b	523 b
Ethephon	433	995 a	668 a	578 a
Chlormequat	463	793 b	601 b	565 ab
		Leger		
Control	447	695 c	527 b	481 b
Ethephon	477	976 a	731 a	474 b
Chlormequat	485	778 b	593 b	529 a
Cultivar x PGR	NS	NS	NS	*

† Means in the same cultivar within the same column followed by different letter(s) are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

* Significant at $P \leq 0.05$.

Table 5.4. Means of stand counts or least square means of shoots m^{-2} at different stages of investigation as affected by plant growth regulator (PGR) by application stage (ZGS) in 1989

PGR treatment	Application stage (ZGS)	Plant stage at investigation: ZGS 12	ZGS 32	ZGS 51	ZGS 90
		No. m^{-2}			
Control		445	699† c	545 cd	502 b
Ethephon	13	476	1145 a	656 b	570 ab
Ethephon	30	455	526 d	865 a	591 a
Ethephon	39	434	649 c	584 bcd	415 c
Chlormequat	13	501	799 b	598 bcd	578 a
Chlormequat	30	474	772 b	623 bc	536 ab
Chlormequat	39	446	709 bc	530 d	526 ab
PGR x ZGS		NS	*	**	**

† Means in the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

*, ** Significant at $P \leq 0.05$ or 0.01, respectively.

Table 5.5. Means of stand counts or least square means of shoots m^{-2} at different stages of investigation as affected by plant growth regulator (PGR) treatment within cultivar in 1990

PGR treatment	Plant stage at investigation			
	ZGS 12	ZGS 32	ZGS 51	ZGS 90
	No. m^{-2}			
		Cadett		
Control	418	899†b	898 b	539 a
Ethephon	438	980 a	1149 a	601 a
Chlormequat	436	880 b	871 b	533 a
		Leger		
Control	462	719 a	736 b	488 b
Ethephon	440	785 a	925 a	578 a
Chlormequat	483	730 a	840 ab	630 a
Cultivar x PGR	NS	*	NS	*

† Means in the same cultivar within the same column followed by different letter(s) are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

Table 5.6. Means of stand counts or least square means of shoots m^{-2} at different stages of investigation as affected by plant growth regulator (PGR) by application stage (ZGS) in 1990

PGR treatment	Application stage (ZGS)	Plant stage at investigation: ZGS 12	ZGS 32	ZGS 51	ZGS 90
		No. m^{-2}			
Control		439	806 † b	826 cd	529 c
Ethephon	13	430	940 a	1022 b	540 bc
Ethephon	30	385	825 b	1432 a	643 a
Ethephon	39	502	806 b	739 d	608 a
Chlormequat	13	471	835 b	840 cd	537 bc
Chlormequat	30	491	775 b	879 c	572 abc
Chlormequat	39	488	796 b	803 cd	561 bc
PGR x ZGS		NS	*	**	*

† Means in the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) analysis.

NS Not significant at $P \leq 0.05$.

*, ** Significant at $P \leq 0.05$ or 0.01, respectively.

Preface to Section 6

Section 6 is the material contained in a manuscript by Ma and Smith (1991d) submitted to the Agronomy Journal. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table is presented at the end of the section.

Following the demonstration of main-stem apical development suppression by PGR treatment in Section 4 and the effects on tillering pattern and dynamics in Section 5, the efficiency and economics of use PGR for yield production are addressed in this section.

Section 6

EFFECTS OF TIMING OF CHLORMEQUAT AND ETHEPHON APPLICATION ON GRAIN PRODUCTION OF BARLEY

6.1 Abstract

Several plant growth regulators (PGR) have potential as lodging control agents for spring barley (Hordeum vulgare L.). Plant growth regulator application also tends to increase the number of spike-bearing tillers in barley. The objective of this study was to evaluate the effects of chlormequat (CCC) and ethephon timing on grain yield and related factors contributing to yield. A 4-yr field study using the cultivars, 'Leger' and 'Cadette', was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquept) at the Emile A. Lods Agronomy Research Center, McGill University, Canada, from 1987 to 1990. Treatments consisted of application of CCC (1.2 kg a.i. ha^{-1}) and ethephon (0.48 kg a.i. ha^{-1}) at Zadoks growth stages (ZGS) 13, 30 and 39. Yield components were measured on both a plot and a single stem spike basis with separation of spikes into main culms (MC) and tiller culms (TC) in the latter case. Early application of ethephon at ZGS 30 significantly increased spikes m^{-2}, while CCC applied at ZGS 13 enhanced the grain number per spike. CCC treatment often increased the grain yield of Leger. Ethephon applied at ZGS 39 reduced plant height and lodging, however, it sometimes decreased yield by up to 27 % due to reductions in the number of grains per spike and/or grain weight. These results indicate that under the continental climatic conditions and the management regime of this study, early application

of CCC or ethephon is not justified for grain production, and that caution must be taken when using ethephon for lodging control at the currently recommended rate and stage.

6.2 Introduction

Among synthetic plant growth regulator(s) (PGR) chlormequat (2-chloroethyl trimethylammonium chloride, CCC) and ethephon (2-chloroethyl phosphonic acid) are the most used in agricultural production. Both PGR have the ability to shorten or stiffen cereal culms, and therefore reduce lodging losses in tall cultivars under conditions of high fertility and favorable precipitation. CCC is an anti-gibberillin agent. Its action is through inhibition of cyclization of trans-geranyl-geranyl-pyrophosphate, which leads to a lowered concentration of kaurene (a GA_3 precursor), and therefore, reduced levels of endogenous gibberellins (Jung, 1984). Although CCC has been shown to be less successful in reducing height and lodging in barley, due to poor absorption of CCC and its rapid transport within the barley plant (Skopik and Cervinka, 1967), it may reduce the apical dominance of the main stem, leading to more within-plant uniformity and greater numbers of spike-bearing tillers in crops such as winter and spring barley (Matthews et al., 1981; Cartwright et al., 1985). Ethephon is a synthetic growth regulator that releases ethylene slowly inside plant tissues through a pH-dependent reaction (Warner and Leopold, 1969). The availability of ethephon has greatly increased the use of ethylene in agronomic and horticultural production. Ethylene inhibits the movement of auxin in stem tissues, thereby

reducing auxin's ability to promote stem elongation. Many studies have shown that ethephon can prevent plant lodging in a wide range of species (Dahnous et al., 1982) via an inhibition of stem elongation (Sachs and Hachett, 1972), leading to reduced plant height.

Chlormequat in wheat, and ethephon in barley, have been widely tested and marketed in Europe for yield protection through lodging control, and recently have been registered for use in some regions of North America (Wiersma et al., 1986). However, yield increases following CCC or ethephon treatment are not consistent (Paterson et al., 1983), which has restricted their large-scale use (Leary and Oplinger, 1983). Moreover, yield reductions due to these PGR have been reported for spring barley, winter barley (Paterson et al., 1983), and corn (Zea mays L.) (Gaska and Oplinger, 1988). For example, in Scotland, a 4 year regional test showed that application of ethephon was generally ineffective with only 11 % of the treatments resulting in an economic increase in barley grain yield. Application of chlormequat and Terpal C (a 2:1 mixture of chlormequat and ethephon) on spring and winter barley resulted in an economic increase in grain yield in only 36 % and 20 % of treatments, respectively. Furthermore, a statistically significant yield reduction due to chlormequat and ethephon was found in 16 % and 17 % of treatments, respectively. Brown and Earley (1973) showed that application of ethephon to oat resulted in a grain yield reduction. Green et al. (1988) reported that mepiquat chloride (1,1 - dimethyl - piperidinium chloride), which produces effects similar to chlormequat, had the potential to increase grain yield only under conditions of

lodging.

For lodging control, the recommended development stages for PGR application are from Zadoks' (Zadoks et al., 1974) growth stages (ZGS) 30 to 31 for CCC and ZGS 37 to 45 for ethephon (Caldwell et al., 1988; Thomas, 1982). Some recent studies demonstrated that early application of these PGR can enhance grain yield without effects on plant height or lodging (Matthews et al., 1981; Waddington and Cartwright, 1986). Early application of ethephon has been demonstrated to increase the number of spike-bearing tillers (Section 7), and to decrease the number of grains per spike (Hill et al., 1982; Brown and Earley, 1973) with little effect on grain weight or yield (Section 7). On the other hand, several studies have shown that even with lodging early application of CCC to spring barley (Koranteng and Matthews, 1982), or winter barley (Matthews et al., 1981) increased the number of spike-bearing tillers and grain yield. This offers a new and potentially powerful strategy in the use of CCC as a yield promoter, rather than a lodging inhibitor (yield protector). In this case the CCC is applied for the modification of plant growth and development, leading to increased yields.

Grain yield differences among treatments can be attributed to differences in the three primary components that make up grain yield, number of spikes per plant or per unit area, number of grains per spike, and mean grain weight. Previous studies have addressed the plant characters and grain yield responses to PGR application (Caldwell et al., 1988; Wiersma et al., 1986; Dahnous et al., 1982; Matthews et al., 1981). Information on yield component alteration due

to PGR treatment and their direct effects on the formation of grain yield is limited. Early application of CCC or ethephon has been shown to temporarily retard the development of main-stem apices, and to lead less tip abortion of the main-culm spike (Section 4). These may release the tillers from apical dominance and thereby produce a higher number of spike-bearing tillers and/or produce greater number of grains per spike. The objective of this study was to evaluate under continental climatic field conditions, the effects of chlormequat and ethephon, at normal rates of application (Thomas et al., 1982) on agronomic variables, yield components and grain yield, when applied at three physiological stages: 1) the beginning of tillering (ZGS 13), 2) the onset of stem elongation (ZGS 30), or 3) the appearance of flag-leaf ligule (ZGS 39).

6.3 Materials and Methods

A 4-yr study on the effects of CCC and ethephon timing of application to spring barley cultivars was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquat) at the E. A. Lods Agronomy Research Center, Macdonald College of McGill University, Quebec, Canada. Meteorological data, field management and experimental design for 1987, 1988, and 1989 have been reported previously (Section 4). Briefly, the climatic conditions were more or less normal in 1989 and 1990, while cooler in 1987, and warmer and drier in 1988 than the 15-yr averages (Section 3). The previous crops were barley in 1987, alfalfa (Medicago sativa L.) in 1988, oat in 1989, and barley in 1990. In each case, the land received a basal dressing of 300 kg ha^{-1} of 5-

9-17 NPK commercial fertilizer prior to seeding. Thirty kg ha^{-1} in 1988 and 100 kg ha^{-1} in all other seasons respectively, of ammonium nitrate N were broadcast onto the plots immediately after seeding. Each plot was 4.2 m long at seeding and consisted of 22 rows at a 10 cm spacing. Prior to harvest these were trimmed back to 3.4 m, to eliminate edge effects along the pathways between blocks. Certified seed treated with Vitaflo was planted at approximately 450 seeds m^{-2}, using a tractor-drawn Kincaid cone-type plot seeder on May 3, in both 1987 and 1988; May 1, 1989 and 1990. In each year the actual seeding density was between 400 and 450 plants m^{-2}. For weed control a mixture of 280 g a.i. ha^{-1} bromoxynil and 646 g a.i. ha^{-1} diclofop-methyl was applied at Zadoks' growth stage (ZGS) 12.

Application of CCC or ethephon was made with a Roper lawn tractor connected to an 80 L tank in 1987 and 1988, and by means of a backpack sprayer in 1989 and 1990. In all cases application was through a boom fitted with four Tee-jet 8002 flat fan nozzles, and with a spray width of 1.1 m. The spray volume was 345 L ha^{-1}, at a pressure of 207 kPa. Citowett Plus at 0.05 % (v/v) was used as a surfactant. During spraying, the target plot was surrounded by a portable plastic barrier to prevent PGR drift into adjacent plots.

Each plot was initially divided into two halves: the first 11 rows were used for taking samples for the determination of apical development stages (Section 4); the remaining 11 rows for measuring yield. Shortly after seedling emergence a 1-meter section in the third row of each plot was marked, and stand counts were made in this section and converted to number of plants m^{-2}. Plant heights and

Belgian lodging scores (Oplinger and Wiersma, 1984) were determined at ZGS 83, and the lodging score was again measured at 1 d prior to harvest. The lodging index for each plot was calculated from the average of these two readings. At crop maturity the previously marked 1-m section was hand harvested, by uprooting or cutting at ground level, for determination of the number of spikes m^{-2}, the number of grains per spike, and harvest index. After trimming the remainder of the plot (3.4 x 1.1 m) was combine harvested for yield determination. The combined plot yield was converted to Mg ha^{-1} on a 14.5 % moisture basis. Samples for 1000-grain weight determinations were drawn from the plot yield sample, counted with an electronic seed counter, and weighed. The number of spikes in the hand-harvested 1-meter section were counted and converted to spikes m^{-2}. In this case a spike refers to a culm with at least one fully-filled seed in the spike. After harvest plants from the 1-meter sample were air-dried at approximately $40^{o}C$ for 10 d. The dried plants were weighed to determine the above-ground biomass, and then threshed to determine the grain weight. Harvest index (HI) (wt. of grain / wt. of above-ground biomass) was determined from the meter samples. The total number of grains in the meter section plants was counted, and grains per spike was calculated from the total number of grains divided by the total number of spikes in the sample.

In order to determine more precisely the effects of the PGR on grain yield and yield components, main culm (MC) spikes and tiller culm (TC) spikes were separated. Using the 1-meter sample, number of spikes m^{-2}, number of grains per spike, 1000-grain weight, and

harvest index were measured separately for main culm spikes and tiller spikes. Therefore, the yield components of the plot and separated MCs and TCs were all derived from the same sample, except for 1000-grain weights which were drawn from the plot yield samples as described above.

Data were analyzed with the SAS system (SAS Institute, 1985). For each measurement, experimental error variances from each year were tested for homogeneity using Bartlett's test (Gomez and Gomez, 1984). A combined analysis of variance across the years 1988 to 1990 was performed and reported if the error variances were homogeneous. The F-test (Steel and Torrie, 1980) was used to determine whether the variations caused by treatments and their interactions were significant. Probabilities of less than or equal to 0.05 were considered significant for main effects and interactions. An F-protected least significant difference ($LSD_{0.05}$) was calculated to compare means of variables found to vary significantly. Within each cultivar the values of control plots for each application stage were pooled, for an overall control mean. Stand count was used as a covariable to adjust for any effect of uneven seeding on yield components, and least square means of cultivar, ethephon rate and their combinations were presented if the covariable had a significant effect.

6.4 Results and Discussion

In 1987, neither grain yield nor yield components were significantly affected by PGR treatment. Interactions of PGR by application stages were not significant for any of the variables measured. In 1988, 1989 and 1990 significant effects due to PGR treatments and their interactions were measured. As the variation of the error mean square for these variables was homogeneous a combined analysis across the years 1988 to 1990 for each agronomic variable investigated was performed, and the results are presented in Table 6.1. There were significant three-way interactions ($P \leq 0.01$) for year, PGR and application stage for all the variables measured with an exception of 1000-grain weight. Thus it was fair to discuss these variables in terms of PGR treatment by application stage each year. For grain yield, plant height and lodging index, the mean of PGR treatment by application stage was compared for each cultivar within each year as 4-way interactions occurred for these variables ($P<0.10$).

Grain yields

Means of grain yield for PGR treatment and application stage within cultivars and years are presented in Table 6.2. In 1987, there was no significant effect of PGR on grain yield. On average the grain yield was 5.17 Mg ha^{-1} for the unsprayed control, 5.55 Mg ha^{-1} for CCC treatment, and 5.46 Mg ha^{-1} for ethephon treatments. The slight increment in grain yield in PGR treated plots was associated with an enhancement of the numbers of spikes m^{-2} though the increase was not significant ($P>0.2$; data not shown). For Leger, application of CCC at

any stage tested significantly increased grain yield in 1988, while grain yield was increased by CCC only at ZGS 30 in 1989. Such an effect did not appear in 1990 when severe lodging occurred. Application of ethephon at ZGS 13 significantly increased grain yield for Leger under the very dry and hot climatic conditions of 1988. During other seasons grain yields were significantly reduced by ethephon at ZGS 30 for both cultivars, at ZGS 13 for Cadette in 1989, and at ZGS 39 for both cultivars in 1989 and for Cadette only in 1990.

In general, ethephon applied at the recommended rate and application stage for lodging control sometimes showed a deleterious effect on grain yield. This is contrary to the findings of Dahnous et al. (1982), and Caldwell et al. (1988). It should be noted that the work of Dahnous et al. (1982) was conducted at Pullman, Washington and ethephon was applied at late 'boot' stage, and the work of Caldwell et al. (1988) was conducted in Nova Scotia, Canada. In both cases the climatic conditions are humid and essentially maritime. It should also be noted that control plots yielded well under lodging conditions in both 1989 (slight lodging) and 1990 (severe lodging). The harvestable yield of lodged crops would probably have been much less in field scale production conditions; our lodged barley plants were harvested at a much lower height and with more care than would be possible for a commercial farmer. Ethephon applied at ZGS 39 effectively controlled lodging (Table 6.7) for the tall cultivar Leger. Grain yield was, however, reduced by more than 27 % under the less severe lodging conditions of 1989. Therefore, caution must be taken when using ethephon as a practical measure for lodging control

under continental climatic conditions such as those under which this study was conducted. Chlormequat, on the other hand, did not prevent plant lodging, but often increased grain yield. Both PGR had a suppression effect on the main culm apices (Section 4). Ethephon treatment showed prolonged effects on MC even at the latest stage of application, which led to some MC spikes developing much behind the control plants. In extreme cases the MC was completely suppressed. The number of MC spikes per unit land area was significantly reduced by ethephon, but not by CCC, which might explain the variation of grain yield due to application of these PGR. Chlormequat temporarily retarded MC apices at earlier stages of apical development. The apices caught up later, near heading, which probably aided in the development of the primary tillers and the tip spikelets of the MC spikes.

Factors Contributing to Yield

The number of spike-bearing shoots m^{-2} was an important component for grain yield. Its production, survival and contribution to grain yield was discussed elsewhere (Section 5). Table 6.3 shows the means of grains per spike, 1000-grain weight, and harvest index as influenced by PGR treatment and application stage in different years.

In 1988 the number of grains per spike was significantly increased by ethephon at ZGS 30, and by CCC at all the stages tested. It should be noted that the number of grains per spike was much lower in 1988 than in the other seasons; this was probably caused by the very low precipitation and hot conditions in that year (Section 7). Ethephon

applied at ZGS 39, in both 1989 and 1990, or at ZGS 30 in 1989, markedly reduced the number of grains per spike, which contributed most to the reduction in grain yields of Cadette in both 1989 and 1990.

In general, 1000-grain weight was little affected by CCC treatment. In contrast, ethephon treatment, except when applied at ZGS 13 in 1988 and at ZGS 39 in 1989, reduced the 1000-grain weight in all cases. These findings were very different from some previously reported (Green, 1986; Harris, 1984) but similar to those of Simmons et al., (1988).

Harvest index is a variable indicating the efficiency of partitioning assimilates to the grain, which is not a primary component of grain yield. In this study harvest index was increased by CCC at ZGS 13 and ZGS 39 in 1988, while it was not affected by these PGR at any application stage during the other seasons. Ethephon treatment often reduced harvest index, particularly when applied at ZGS 30 or ZGS 39, as was the case in both 1989 and 1990.

Attempts to explain the yield effects in terms of the effect of PGR on yield components were complicated by the fact that over years, there was no consistent response of any component to PGR treatments. The conditions (temperature and moisture) at the time of and immediately after PGR application may have influenced the rate of absorption and thus the response of yield to these PGR (Simmons et al., 1988).

Separation of spikes into main- and tiller-culms revealed that the interaction of PGR treatment and application stage on MC spikes

was quite different from that on TC spikes, though the pattern of significance was similar (Table 6.4). The means of spikes m^{-2}, adjusted for plant density, means of grains per spike, 1000-grain weight, and harvest index based on MC- and TC-spikes as affected by PGR x application stage within years are presented in Table 6.5. It was clearly shown that application of CCC did not markedly affect any of these components in the tiller culms while ethephon generally increased these variables in TC. The increments in the components of TC were partially or completely compensated for by the reduction in these components of MC. Since the MC spike was the major component contributing to grain yield per plant or per ha, the overall effect of ethephon applied at ZGS 30 or ZGS 39 on yield components was a reduction in the grain yield in 1989 and 1990, especially in the case of Cadette.

Plant Characters

In 1988 application of ethephon at ZGS 39 delayed maturity by approximately 3 d while heading date was only slightly extended by this PGR. Application of ethephon at both ZGS 30 and ZGS 39 delayed heading by 2 to 3 d in 1989 and 1990, and maturity by 3 to 4 d in 1989. In contrast, application of CCC at any stage tested did not significantly affect days to heading or to maturity (Table 6.6). These data disagree with Green (1986), who found that application of CCC to spring barley could extend the period of grain fill.

Plant height was significantly reduced by PGR treatment. There was a significant interaction of PGR treatment and application stage

within cultivar each year. Application of ethephon at ZGS 30 or ZGS 39 decreased plant height by 9 to 21 cm for Cadette in both 1989 and 1990, and by 5 to 32 cm for Leger (Table 6.7). In 1989, application of CCC to Cadette at ZGS 30 or ZGS 39 and to Leger at all application stages also significantly reduced plant height. However, the standing ability was improved only by ethephon application at ZGS 39 for the standard tall cultivar, Leger. Early application of ethephon, at ZGS 13 or ZGS 30, and application of CCC at ZGS 30 slightly yet significantly increased lodging in Cadette, a semi-dwarf cultivar, under the severe lodging conditions of 1990. These results agreed with those previously reported (Dahnous et al., 1982; Simmon et al., 1988).

In summary, early application of ethephon, at ZGS 30, often increased the number of spikes m^{-2} while CCC applied at ZGS 13 enhanced the number of grains per spike, and early application of either PGR sometimes increased grain yield. In general, CCC showed fewer detrimental side effects on the barley cultivars tested than did ethephon. Plant height and lodging was reduced by ethephon applied at ZGS 39, however, this sometimes reduced grain yields due to the suppression on MC spikes.

Table 6.1. Combined analyses of variances: Probabilities for the effect of treatments on agronomic traits of two barley cultivars over 3 seasons, 1988-1990.

Source	df	Grain yield	Grains spike^{-1}	1000-grain weight	Harvest index	Plant height	Lodging index	Days from seeding to Heading	Days from seeding to Maturity
Year (Y)	2	0.0001	0.0001	0.06	0.001	0.0001	0.0001	0.0001	0.0001
Error A	9								
Cultivar (C)	1	0.3	0.0001	0.0002	0.001	0.0001	0.0001	0.0001	0.0001
PGR† (P)	2	0.0001	0.0001	0.8	0.0001	0.0001	0.007	0.0001	0.0001
ZGS‡ (Z)	2	0.0001	0.0001	0.7	0.0001	0.0001	0.0002	0.0001	0.0006
Y x C	2	0.0001	0.0001	0.3	0.0001	0.0001	0.0001	0.0001	0.0001
Y x P	4	0.0001	0.0001	0.02	0.0001	0.0001	0.2	0.0001	0.0001
Y x Z	4	0.003	0.0007	0.7	0.0001	0.001	0.3	0.0001	0.0009
C x P	2	0.0001	0.9	0.9	0.6	0.2	0.0001	0.4	0.0001
C x Z	2	0.4	0.5	0.9	0.5	0.4	0.07	0.6	0.9
P x Z	4	0.0001	0.0001	0.7	0.0001	0.0001	0.0003	0.001	0.01
Y x C x P	4	0.02	0.8	0.9	0.1	0.2	0.4	0.5	0.7
Y x C x Z	4	0.3	0.6	0.8	0.3	0.5	0.7	0.4	0.4
Y x P x Z	8	0.0001	0.004	0.7	0.0001	0.0001	0.0001	0.0001	0.0003
C x P x Z	4	0.3	0.8	0.9	0.6	0.12	0.01	0.3	0.4
Y x C x P x Z	8	0.09	0.8	0.9	0.6	0.09	0.02	0.6	0.7
Error B	152								
C.V. (%)		10.4	14.9	16.7	9.3	5.8	55.1	2.1	1.5

† PGR = Plant growth regulator treatment.

‡ ZGS = Zadoks growth stage.

Table 6.2. Means of grain yield as affected by plant growth regulator (PGR) treatment and application stage (ZGS) within cultivar in 1987, 1988, 1989 and 1990.

Treatment		Grain yield (Mg ha^{-1})			
PGR	ZGS	1987†	1988	1989	1990
			Cadette		
Control		5.23	3.15‡b	7.39 a	7.07 a
Ethephon	13	5.67	3.21 ab	6.53 b	6.63 a
Ethephon	30	-	3.26 ab	6.38 b	4.90 b
Ethephon	39	5.49	2.73 b	3.33 c	4.70 b
CCC	13	5.62	3.47 a	7.13 a	6.57 a
CCC	30	-	2.99 ab	6.95 a	6.94 a
CCC	39	5.89	3.37 a	6.78 a	6.80 a
			Leger		
Control		5.11	3.85 bc	6.14 b	6.48 ab
Ethephon	13	5.40	4.58 a	6.00 b	6.15 b
Ethephon	30	-	3.54 c	6.12 b	5.28 c
Ethephon	39	5.18	4.21 ab	4.45 c	6.17 b
CCC	13	5.05	4.36 ab	6.49 ab	6.82 a
CCC	30	-	4.39 ab	6.94 a	6.91 a
CCC	39	5.68	4.50 a	6.28 b	6.44 ab

† Grain yield was not significantly different by F-test ($P \leq 0.05$) in 1987.

‡ Means of the same cultivar within the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) test.

Table 6.3. Means of grains spike^{-1}, 1000-grain weight (g), and harvest index as affected by plant growth regulator (PGR) treatment and application stage (ZGS) in 1988, 1989 and 1990.

Source PGR	ZGS	Grains spike^{-1}	1000-Grain wt (g)	Harvest index
			1988	
Control		14.1† c	38.3 a	0.395 cd
Ethephon	13	16.6 bc	37.5 ab	0.363 cd
Ethephon	30	19.5 ab	36.5 bc	0.401 bcd
Ethephon	39	16.5 bc	35.5 c	0.359 d
CCC	13	19.3 b	38.3 a	0.436 ab
CCC	30	18.4 b	38.4 a	0.417 abc
CCC	39	22.5 a	38.9 a	0.453 a
			1989	
Control		38.8 a	39.0 ab	0.471 a
Ethephon	13	37.2 a	36.0 c	0.457 a
Ethephon	30	32.3 b	36.9 c	0.401 b
Ethephon	39	16.3 c	40.1 a	0.167 c
CCC	13	39.4 a	39.1 ab	0.481 a
CCC	30	39.8 a	38.5 b	0.473 a
CCC	39	40.2 a	39.3 ab	0.490 a
			1990	
Control		33.5 ab	39.8 a	0.509 ab
Ethephon	13	31.8 b	37.0 b	0.477 b
Ethephon	30	32.5 b	27.6 d	0.388 c
Ethephon	39	20.6 c	34.0 c	0.363 c
CCC	13	36.0 a	38.6 a	0.508 ab
CCC	30	33.3 ab	39.0 a	0.518 a
CCC	39	33.8 ab	39.1 a	0.516 a

† Means of the same cultivar within the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) test.

Table 6.4. Combined analyses of variances: Probabilities for effects of treatments on agronomic traits of two barley cultivars over 3 seasons, 1988-1990. (Separation of main-culm spike (MC) and tiller-culm spike (TC)).

Source	df	Spikes m^{-2}		Grains spike^{-1}		1000-Grain weight		Harvest index	
		MC	TC	MC	TC	MC	TC	MC	TC
Year (Y)	2	0.9	0.0003	0.0001	0.0001	0.0001	0.0001	0.03	0.0001
Error A	9								
Cultivar (C)	1	0.001	0.0001	0.0001	0.4	0.0001	0.0001	0.07	0.7
PGR†(P)	2	0.4	0.0001	0.0001	0.7	0.0001	0.003	0.0001	0 06
ZGS‡(Z)	2	0.0001	0.0001	0.0001	0.0001	0.0001	0.400	0.0001	0.0001
Y x C	2	0.01	0.02	0.2	0.01	0.06	0.200	0.0001	0.03
Y x P	4	0.02	0.001	0.0001	0.0001	0.0001	0.001	0.0001	0.0001
Y x Z	4	0.001	0.02	0.001	0.0001	0.0001	0.060	0.0001	0.0001
C x P	2	0.2	0.8	0.6	0.6	0.1	0.3	0.3	0.9
C x Z	2	0.4	0.02	0.5	0.4	0.3	0.5	0.1	0.4
P x Z	4	0.9	0.002	0.0001	0.0001	0.0001	0.04	0.0001	0.0001
Y x C x P	4	0.01	0.06	0.6	0.8	0.06	0.4	0.09	0.4
Y x C x Z	4	0.06	0.3	0.9	0.3	0.7	0.9	0.2	0.6
Y x P x Z	8	0.01	0.001	0.0002	0.0001	0.0001	0.09	0.0001	0.0001
C x P x Z	4	0.1	0.4	0.9	0.8	0.01	0.7	0.1	0.7
Y x C x P x Z	8	0.3	0.1	0.5	0.2	0.04	0.7	0.6	0.1
Error B	152								
C.V.		15.1	47.5	14.1	26.6	5.4	15.7	10.1	26.6

† PGR = Plant growth regulator treatment.

‡ ZGS = Zadoks growth stage.

Table 6.5. Least square means of spikes m^{-2} and means of grains $spike^{-1}$, 1000-grain weight (g), and Harvest index as affected by plant growth regultor (PGR) treatment and application stage (ZGS) in 1988, 1989 and 1990. (Separation of main-culm spike (MC) and tiller spike (TC)).

Source		Spikes m^{-2}		Grains $spike^{-1}$		1000-Grain weight		Harvest index	
PGR	ZGS	MC	TC	MC	TC	MC	TC	MC	TC
					1988				
Control		345† a	106 b	19.9 bc	9.4 a	40.9 a	20.3 a	0.431 bc	0.180 c
Ethephon	13	338 a	127 ab	18.6 bc	9.1 a	41.2 a	21.1 a	0.393 c	0.203 bc
Ethephon	30	337 a	148 ab	22.3 abc	11.5 a	40.0 a	21.0 a	0.421 bc	0.302 a
Ethephon	39	378 a	191 a	17.9 c	13.9 a	41.1 a	22.1 a	0.385 c	0.269 ab
CCC	13	353 a	107 b	22.8 ab	10.4 a	41.0 a	20.8 a	0.464 ab	0.248 abc
CCC	30	377 a	159 ab	22.4 ab	9.6 a	41.6 a	21.2 a	0.453 ab	0.245 abc
CCC	39	340 a	128 ab	25.4 a	11.0 a	41.5 a	20.5 a	0.482 a	0.218 abc
					1989				
Control		421 a	81 b	40.5 a	30.7 a	37.0 ab	32.1 a	0.469 a	0.482 a
Ethephon	13	433 a	137 b	39.7 a	28.1 a	33.9 c	28.7 a	0.460 a	0.435 a
Ethephon	30	352 b	240 a	35.0 b	29.1 a	35.3 bc	31.9 a	0.383 b	0.422 a
Ethephon	39	314 b	101 b	17.8 c	10.3 b	36.1 ab	22.9 b	0.189 c	0.082 b
CCC	13	464 a	114 b	41.9 a	27.9 a	35.9 ab	30.6 a	0.487 a	0.450 a
CCC	30	426 a	110 b	42.2 a	29.3 a	35.3 ab	30.4 a	0.474 a	0.464 a
CCC	39	440 a	85 b	42.3 a	28.7 a	37.3 a	33.7 a	0.491 a	0.463 a
					1990				
Control		428 a	101 c	39.3 ab	15.5 cd	39.6 a	25.9 a	0.526 ab	0.351 ab
Ethephon	13	423 a	122 c	35.2 b	19.3 bc	35.2 b	24.2 ab	0.484 b	0.399 ab
Ethephon	30	281 c	369 a	22.1 c	32.8 a	24.1 c	22.7 ab	0.341 c	0.416 a
Ethephon	39	340 b	269 b	20.6 c	17.1 bcd	37.8 a	21.3 b	0.362 c	0.284 b
CCC	13	426 a	113 c	39.9 a	21.4 b	38.2 a	24.1 ab	0.517 ab	0.437 a
CCC	30	450 a	124 c	38.5 ab	12.8 d	39.2 a	19.9 b	0.532 a	0.294 b
CCC	39	435 a	128 c	38.4 ab	16.6 bcd	38.6 a	22.1 b	0.531 a	0.326 b

† Means of the same cultivar within the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) test.

Table 6.6. Means of the number of days from seeding to heading and maturity as affected by plant growth regulator (PGR) treatment and application stage (ZGS) in 1988, 1989 and 1990.

		Heading			Maturity		
PGR	ZGS	1988	1989	1990	1988	1989	1990
Control		49.5† a	56.6 c	56.9 c	85.1 bc	87.2 b	89.6 ab
Ethephon	13	50.0 a	58.5 b	59.1 b	84.9 c	87.0 b	90.3 ab
Ethephon	30	49.5 a	59.0 a	64.8 a	85.0 c	90.3 a	90.6 a
Ethephon	39	50.5 a	59.8 a	58.5 b	87.9 a	91.0 a	89.3 b
CCC	13	50.2 a	56.8 c	56.8 c	86.3 b	86.8 b	89.6 ab
CCC	30	50.0 a	57.3 c	57.3 c	86.3 b	87.0 b	90.3 ab
CCC	39	49.0 a	56.5 c	57.0 c	85.1 bc	87.3 b	89.8 ab

† Means of the same cultivar within the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) test.

Table 6.7. Means of plant height (cm) and Belgian lodging index as affected by plant growth regulator (PGR) treatment and application stage (ZGS) within cultivar in 1988, 1989 and 1990.

Treatment		Plant height			Belgian lodging index		
PGR	ZGS	1988	1989	1990	1988	1989	1990
				Cadette			
Control		46†ab	84 a	80 a	0.2 a	0.2 a	0.5 c
Ethephon	13	45 b	78 cd	78 a	0.2 a	1.0 a	2.7 a
Ethephon	30	49 a	75 d	70 b	0.2 a	0.2 a	2.3 a
Ethephon	39	45 b	65 e	59 c	0.2 a	0.2 a	0.2 c
CCC	13	45 b	82 ab	77 a	0.2 a	0.4 a	0.6 c
CCC	30	43 c	80 bc	79 a	0.2 a	0.2 a	2.1 ab
CCC	39	48 ab	77 c	78 a	0.2 a	0.2 a	1.0 bc
				Leger			
Control		50 a	106 a	95 a	0.2 a	3.8 a	8.1 a
Ethephon	13	52 a	96 c	98 a	0.2 a	0.5 c	8.0 a
Ethephon	30	45 b	96 c	86 b	0.2 a	2.6 ab	8.5 a
Ethephon	39	45 b	74 d	75 c	0.2 a	0.2 c	0.2 b
CCC	13	49 ab	100 b	96 a	0.2 a	4.0 a	8.0 a
CCC	30	48 ab	93 d	95 a	0.2 a	1.3 bc	8.0 a
CCC	39	51 a	99 b	96 a	0.2 a	1.7 b	7.5 a

† Means of the same cultivar within the same column followed by different letters are significantly different by a protected LSD ($P \leq 0.05$) test.

Preface to Section 7

Section 7 is the material contained in a manuscript by Ma and Smith (1991g) published in the Journal of Agronomy and Crop Science. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table is presented at the end of the section.

The previous three sections addressed the response of spring barley to the application of single PGR (CCC or ethephon) treatment. Section 7 deals with early application of ethephon alone or in combination with chlormequat on the number of spike-bearing shoots and the contribution of this variable to grain yield.

Section 7

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.)

7.1 Abstract

Effects of chlormequat chloride (CCC), ethephon and mixtures of CCC and ethephon, applied at Zadoks growth stage (ZGS) 30 (the beginning of stem elongation) on the number of spike-bearing shoots and their contribution to grain yields of four spring barley (Hordeum vulgare L.) cultivars were studied in 1987 and 1988 at McGill University, Quebec, Canada. The results varied between years and among cultivars. The mixtures of CCC and ethephon or ethephon alone, produced significant increases in the number of spikes m^{-2} in cultivars Joly and Laurier, in both years, and in Leger only in 1988. Ethephon and ethephon containing mixtures reduced the yields of Joly and Leger in 1988. In both years CCC had no effect on spikes m^{-2} for all cultivars. Increases in spikes m^{-2} were accompanied by decreases in 1000-grain weight, and/or grains per spike, which offset or more than offset potential benefits from increased spikes m^{-2}. These results indicate that under continental climatic conditions such as those prevalent in Quebec, Canada, application of PGR to spring barley at ZGS 30 does not increase grain yield through an increased number of spikes m^{-2}.

7.2 Introduction

Spring barley (Hordeum vulgare L.) is the major small grain crop produced in Quebec, Canada. It is usually produced using moderate nitrogen fertilizer applications. In Europe, cereal producers have been using more intensive management strategies, involving increased N fertilizer use and fungicides, since the 1960's. High N fertility promotes lodging in cereals, but the use of plant growth regulator(s) (PGR) as antilodging agents can reduce lodging and aid in maintaining yield potential (Green, 1986; Dahnous et al., 1982). With early application, PGR have also been used to enhance grain yield in winter barley by increasing the number of spike-bearing shoots per unit area (Matthews et al., 1981), thereby increasing yield potential. Information dealing with the early application of PGR combinations in North America is limited.

Chlormequat chloride (2-chloroethyl trimethylammonium chloride, chlorocholine chloride, CCC or Cycocel, a tradename), was introduced as an antilodging agent for wheat (Triticum aestivum L.) (Cyanamid, 1966). By inhibiting the formation of a gibberellin precursor (Williams et al., 1982; Gale 1978), it shortens the basal internodes of cereal culms (Koranteng and Matthews, 1982) and has been widely used to minimize lodging in wheat. Koranteng and Matthews (1982) reported that early application of CCC to spring barley also increased grain yields in pot and small-plot field experiments. CCC decreases the competitiveness of developing sinks, leading to more spike-bearing tillers in barley (Koranteng and Matthews, 1982) and to a more

synchronous spikelet development within a spike in both wheat and barley (Höfner and Kühn, 1982). Matthews and Caldicott (1981) demonstrated that CCC-treated plants had greater within-plant uniformity both in tiller-spike size and grain size. Thus it may be possible to use CCC as a yield promoter, rather than a lodging inhibitor, in order to increase the number of spike-bearing tillers and/or to produce a higher number of grains per spike, thus improving the effective utilization of available resources.

Ethephon (2-chloroethyl phosphonic acid, or tradenames: Cerone, Ethrel or Camposan), which releases ethylene at pH 5 or higher (Warner and Leopold, 1969), has been shown to reduce plant height and lodging in barley (Dahnous et al., 1982). Application at ZGS 13 can result in a greater number of spikes m^{-2} (Cartwright and Waddington, 1981), accompanied by an increase (Harris, 1984), or decrease (Simmons et al., 1988; Brown and Earley, 1973) in grain number per spike.

The commercial mixture of chlormequat chloride and ethephon at a ratio of 2:1 (tradename, Terpal C), is another straw-shortening product used in Europe (Caldwell et al., 1988; Caldwell and Starratt, 1987). Much less has been published on the effects of this growth regulator on spike-bearing shoots and grain yields. Under drought stress conditions, such as those regularly encountered in continental North America, CCC might be more effective on barley than ethephon since the former has been reported to improve water use efficiency (Green, 1986) while the latter usually decreases water and osmotic potential (Kirkham, 1983) and accelerates senescence of plants (Yang and Hoffman, 1984). Thus, the effect of different ratios of these two

components on the number of spike-bearing shoots and their association with other yield components and grain yields are of interest.

The recommended growth stages for chlormequat chloride, ethephon and Terpal C application to cereals are Zadoks (Zadoks et al., 1974) growth stages (ZGS) 30, 37-45, and 33, respectively (Caldwell et al., 1988; Thomas, 1982). Earlier application of chlormequat chloride and ethephon at ZGS 13 has been tested as a method of decreasing the dominance of the main-shoot spike in order to get better synchronization of tiller formation and to increase tiller survival and spike number per unit area (Waddington and Cartwright, 1986; Koranteng and Matthews, 1982; Cartwright and Waddington, 1981; Matthews and Caldicott, 1981). Early application of ethephon has been demonstrated to increase tiller survival and to decrease grain number per spike (Hill et al., 1982; Brown and Earley, 1973). Whether this follows from more spikes with fewer seeds each, a decrease in the number of seeds in the main spike from competition with tillers, or other early effects by the treatment is unknown. Early applications of different ratios of chlormequat chloride and ethephon or ethephon alone at ZGS 30 have not previously been reported for spring barley. This study was initiated with the objective of ascertaining the effects of these PGR on spike-bearing shoots and their contribution to grain yield, in a range of barley cultivars, at the beginning of main stem elongation (ZGS 30).

7.3 Materials and Methods

In 1987 and 1988, experiments to test the effects of PGR applied to

spring barley cultivars at ZGS 30 were conducted on a sandy loam soil at the E. A. Lods Agronomy Research Center of Macdonald College of McGill University, Quebec, Canada. Rainfall for May, June, and July was 72, 116 and 105 mm in 1987, and 47, 75 and 37 mm in 1988, respectively. Average temperatures for these months were 13, 19 and 20 ^{0} C in 1987, and 15, 18 and 23 ^{0} C in 1988, respectively. The 1987 site had produced barley in 1986, and the 1988 site had produced alfalfa (Medicago sativa L.) in 1987. Both sites received a basal dressing of 300 kg ha^{-1} of 5-20-20 commercial fertilizer prior to seeding. In both years, the experiment was a 4 x 6 factorial, arranged in a randomized complete block design with 4 replicates. Each plot was 3.8 m long, with 11 rows spaced 10 cm apart. Plots were seeded at a rate of 450 seeds m^{-2}, using a tractor drawn Kincaid cone-type plot seeder on May 3, 1987 and May 3, 1988. One hundred kg N ha^{-1} in 1987 and 30 kg N ha^{-1} in 1988, as ammonium nitrate, were broadcast onto each plot immediately after seeding. A mixture of 280 g a.i. ha^{-1} bromoxynil and 646 g ha^{-1} diclofop-methyl was applied at ZGS 12. Applications of CCC, ethephon or combinations of the two were made by means of a small lawn tractor fitted with a 275-cm boom connected to an 80-L tank attached to the rear. Two Tee-jet 8002 flat fan nozzles were used to spray a width of 1.1 m with a spray volume 345 L ha^{-1}, at a pressure of 207 kPa. Citowett Plus at 0.05 % (v/v) was used as a surfactant.

Four six-row barley cultivars were used: Laurier, Leger, Cadette and Joly. Plots of these cultivars received one of the following six treatments:

a) chlormequat chloride at 1200 g ha^{-1};

b) ethephon at 480 g ha^{-1};

c) CCC : ethephon at a ratio of 3 : 1 of the formulated product (900 g ha^{-1} CCC with 120 g ha^{-1} ethephon);

d) CCC : ethephon at a ratio of 1 : 1 (600 g ha^{-1} CCC with 240 g ha^{-1} ethephon);

e) CCC : ethephon at a ratio of 1 : 3 (300 g ha^{-1} CCC with 360 g ha^{-1} ethephon);

f) control (no PGR application).

In both years, observations were taken from a section of the third row (a 3-m section in 1987 and a 1-m section in 1988) of each plot: stand counts at ZGS 12; Belgian (Oplinger and Wiersma, 1984) lodging score and lodging index, spikes m^{-2} and grains $spike^{-1}$ at ZGS 83; 1000-grain weight, above-ground biomass and harvest index at maturity. The latter three variables were determined from samples that had been air-dried at 70° C for 48 h. Grain yields were measured in an area of 3.6 m x 1.1 m and converted to T ha^{-1} on a basis of 14.5 % moisture content.

In order to determine more precisely the effects of the PGR on grain yield and yield components in 1988, main culm (MC) spikes and tiller culm (TC) spikes were separated. A tiller spike or a fertile tiller is defined as any tiller with one or more grains. Using the 1-M sample, number of spikes m^{-2} , number of grains per spike, 1000-grain weight, and harvest index were measured separately for main culm spikes and tiller spikes.

Data were analyzed with the SAS system (SAS Institute, 1985).

The F-test (Steel and Torrie, 1980) was used to determine whether the variations caused by treatments and their interactions were significant. An F-protected $LSD_{0.05}$ was calculated to compare means of variables found to vary significantly. A single degree of freedom orthogonal contrast was employed to evaluate the simple effects of PGR within cultivars if a significant interaction effect was found for any yield component variable. In this case, means of PGR within cultivar were compared and presented. Stand count was used as a covariable to adjust for any effect caused by uneven seeding on yield components, and least square means of cultivar, PGR and their combinations were presented if the covariable had a significant effect.

7.4 Results

As a check, prior to the application of PGR, apices from each plot were dissected, and the stages of development were determined. Results showed that no significant differences occurred among treatment plots prior to PGR application although marked differences were noted among cultivars (data not shown).

Both cultivars and PGR affected yield components, grain yield, and agronomic characters. Significant cultivar x PGR interactions were measured for spikes m^{-2}, 1000-grain weight and plant height in both years, and for harvest index and grain yield in 1988 (Table 7.1), indicating that the sensitivities of cultivars to these PGR were different. In addition, growing conditions in 1988 were very different from those in 1987, with a long period of low precipitation and high

temperature occurring after seedling establishment. Under such stress conditions, the average grain yield of all cultivars in 1988 was 40 % lower than in 1987. Thus, the response of cultivars to PGR was also dependent upon years.

In Cadette (Table 7.1), application of any PGR or PGR combination at ZGS 30 had no effect on number of spikes m^{-2} in both years, and plant height and grain yield in 1988. All PGR significantly reduced plant height by 4 to 6 cm in 1987. CCC alone or in combination with ethephon at any of the ratios significantly increased 1000-grain weight in 1988. Harvest index was also slightly but significantly increased by application of CCC or 3:1 and 1:1 ratios in 1988.

Field observations showed that Joly was the most sensitive cultivar to PGR application. In both years ethephon and 3:1, 1:1 CCC:ethephon mixtures significantly increased number of spikes m^{-2} in Joly (Table 7.1). This increase was mainly attributed to an increase in spike-bearing tillers (Table 7.2). The grain yield was, however, significantly decreased by these PGR in 1988, which was associated with a significant reduction in 1000-grain weight. In 1988, plant height was significantly increased, and harvest index was significantly decreased by these PGR through the reduction in main-culm harvest index.

With regard to the changes in number of spike-bearing shoots following PGR application, Laurier responded very similarly to Joly (Table 7.1). For Laurier, with better rainfall in 1987, both ethephon and the 1:3 CCC:ethephon mixture significantly increased number of spikes m^{-2} ; however, this was offset by the reduction in 1000-grain

weight, so that grain yield remained unchanged. Under the dry, hot conditions of 1988, number of spikes m^{-2} was also significantly increased by either ethephon alone or ethephon in combination with CCC. Thousand-grain weight was again reduced by ethephon, 1:1 and 1:3 CCC:ethephon mixtures. For Laurier, grain yield was not affected by PGR in either year. In 1987, plant height was reduced by 5 to 8 cm by PGR. Application of CCC at ZGS 30 did not affect the number of spikes m^{-2} in both seasons, but it did significantly increase 1000-grain weight in 1988. Similar to Joly, Laurier plant height was unusually increased by 3:1 and 1:1 CCC:ethephon mixtures and ethephon alone in 1988, although these PGR resulted in significant reduction in plant height in 1987.

Neither of the tested PGR had any significant effect on the number of spike-bearing shoots in Leger under the higher rainfall conditions of 1987 (Table 7.1). This followed the same pattern as found in Cadette. However, under drought stress conditions of 1988, ethephon and the 3:1 CCC:ethephon mixture significantly increased number of spikes m^{-2}, and decreased grain yield. The yield decrease was due to a reduction in 1000-grain weight. It was also found that CCC alone or the 1:3 CCC:ethephon mixture significantly increased 1000-grain weight in 1987.

The separation of spikes into main- and tiller-culms in 1988 showed that the effects of PGR on main-culm spikes was very different from the effect on tiller-culm spikes (Table 7.2). For example, ethephon and the 3:1 CCC:ethephon mixture decreased the number of spikes m^{-2}, the number of grains $spike^{-1}$, 1000-grain weight and

harvest index for the main culms, but increased all of these variables for tiller culms, except for 1000-grain weight in Joly. Since main culm spikes are the major contributors to grain yield, particularly under stress conditions, the overall response of grain yield to ethephon in 1988 was a reduction. CCC did not improve tiller survival in any of the tested cultivars, but it significantly increased the number of grains spike^{-1} from main culm spikes and 1000-grain weight from tiller culms in Cadette.

There was no significant cultivar x PGR interaction for grains spike^{-1}, lodging index and days to maturity in both years, and harvest index and grain yield in 1987 (Table 7.3). Application of ethephon at ZGS 30 significantly reduced harvest index in 1987, and maturity was delayed by ethephon in both years. Plant lodging occurred in 1987, but not in 1988. Plant growth regulators, applied at ZGS 30, did not improve resistance to lodging (data not shown). In 1987, grain yield was significantly different among cultivars. The ranking was Leger, Cadette, Laurier, Joly, with Leger significantly outyielding Joly. Plant growth regulators did not significantly increase grain yield when compared to the control.

7.5 Discussion

Early applications of mepiquat chloride (1,1-dimethyl-piperidinium chloride) and CCC (Waddington and Cartwright, 1986) or GA_3 , at ZGS 13, (Matthews et al., 1981) can affect the yield components of spring cereals. In this study we found that ethephon and mixtures of CCC and ethephon at different ratios, applied at ZGS 30 significantly

increased number of spikes m^{-2} in two (Joly and Laurier) of four cultivars in both years of the experiment, and in one (Leger) in 1988 only (Table 7.1). Although Caldwell et al. (1988) reported that barley cultivars have different sensitivities to ethephon application at ZGS 37 and/or ZGS 45, the recommended growth stage for application, no data have been published regarding cultivar sensitivity to early application of these PGR. Under drought conditions, these PGR effected a slight decrease in the number of main-culm spikes, and a marked increase in the number of tiller-culm spikes (Table 7.2). The response of cultivars to the application of PGR at ZGS 30 varied. Joly and Laurier showed a significant increase in spikes m^{-2} due to the application of ethephon alone or in combination with CCC, however, this benefit was offset by a reduction in the other yield components. With application of ethephon or 3:1 CCC:ethephon mixture 1000-grain weight was significantly decreased. Joly and Leger showed significant grain yield reductions in 1988 (Table 7.1). The application of CCC at ZGS 30 showed no significant effect on spikes m^{-2} in any of the tested cultivars, in both years. Similar effects have been reported by other workers for application of PGR at the beginning of tillering (ZGS 13). For instance, Scheffer et al. (1983) observed that application of Terpal, whose ingredients are mepiquat chloride and ethephon, at ZGS 13, was capable of increasing yield by raising the number of spikes m^{-2}, while Waddington and Cartwright (1986) observed that early application of CCC at ZGS 13 alone usually had no significant effect on this component.

Plant height was significantly affected by these PGR with little

change in resistance to lodging (lodging data not shown). All tested PGR significantly reduced plant height by 4 to 9 cm in two (Cadette and Laurier) of four cultivars, under reasonable rainfall conditions, and a significant increase in plant height by some of the tested PGR was experienced in Joly and Laurier under moisture-deficit and hot stress conditions (Table 7.1). As the PGR inhibited main-culm development, it is probable that tillers were released from apical dominance, more tillers were produced and were taller than the main culms resulting in the mean plant height being higher than the unsprayed control (Table 7.2). In a related fashion, harvest index was significantly decreased by these PGR, through a reduction in main-culm harvest index during a year of moisture and temperature stress.

It is interesting to note that CCC significantly increased 1000-grain weight in Leger during a better rainfall year, and in Cadette during a drought-stress year, while ethephon application led to a significant reduction of this component in Laurier in both years and in Joly and Leger in 1988 (Table 7.1). This observation contradicts the findings of other workers (Pearson et al., 1989; Green et al., 1985; Harris, 1984). It seems possible that ethephon lessened the apical dominance of the main culms, allowing more tillers to survive, approach or exceed main-culm size, and produce harvestable spikes (Cartwright and Waddington, 1981), while reducing the size of the main culms. Under stress conditions, ethephon had a severe and lasting inhibitory effect on main culm apices. This resulted in some main culms dying back completely, and a marked increment in tiller spike production. This phenomenon was especially obvious for Joly (Table

7.2). Unlike ethephon, CCC did not have deleterious effects on main-culm spikes and did not significantly increase the number of tiller-culm spikes. These observations offer an explanation of the more favourable effects of CCC, under moisture deficit stress conditions, than ethephon.

In a study of spring barley yield component modification by very early application of CCC and mepiquat chloride at ZGS 13, Waddington and Cartwright (1986) ranked barley shoots, and showed that yield improvements measured in the PGR treatments were achieved by increasing spikes plant^{-1}, grains spike^{-1} and the above ground biomass in certain later-formed, lower ranking shoots. They determined changes in spikes plant^{-1} by counting number of fertile tillers at harvest. When evaluating the contribution of tillers to grain yield in winter wheat, Frederick and Marshall (1985) measured the percentage of fertile tillers and total grain weight in a meter-long section of row, and calculated the number of grains per tiller. Data, regarding the effects of the early PGR application on tiller contribution to the yield of spring barley, derived by direct measurement, have not been previously reported. In our study, barley spikes were grouped by main-culm and tiller culm, which allows us to make direct determination of how yield components changed in response to PGR application.

Summary

Results demonstrated that both genetic and climatic factors affected

the response of barley plants to the application of PGR. Under better rainfall conditions, ethephon had a significant influence on the number of spikes m^{-2} in Joly and Laurier when applied at ZGS 30. The application of CCC at this stage showed no significant effect on yield components, except for increments in 1000-grain weight in Leger under reasonable moisture conditions and in Cadette and Laurier under drought stress. Ethephon and the mixtures of CCC with ethephon applied at ZGS 30, under drought stress conditions, increased spikes m^{-2} by producing more productive tiller spikes, but this effect was more than offset by the reduction in other yield components and, as a result, the overall effect was a reduction of grain yield in Joly and Leger. This reduction was mainly due to the retardant effect of PGR on main culm spikes. Overall, the application of ethephon alone or ethephon containing PGR at the beginning of stem elongation is effective in increasing the number of spikes m^{-2} through an increment in spike-bearing tillers in most cultivars tested, but does not increase grain yield.

Table 7.1. Means of variables as affected by cultivar and PGR combinations

Source	Spikes[‡] m^{-2}		1000-grain wt. (g)		Plant height (cm)		Harvest index	Grain yield (t ha^{-1})
	1987	1988	1987	1988	1987	1988	1988	1988
				Cadette				
Control	461[†] a	512 a	40.0 a	28.3 c	76 a	45 a	0.303 b	2.6 a
CCC	505 a	505 a	38.1 ab	33.8 ab	70 b	47 a	0.378 a	2.8 a
3:1	435 a	543 a	37.1 ab	34.3 ab	71 b	48 a	0.368 a	2.2 a
1:1	452 a	518 a	36.6 b	34.0 ab	70 b	49 a	0.382 a	2.7 a
1:3	492 a	475 a	38.0 ab	37.4 a	72 b	48 a	0.355 ab	2.5 a
Ethephon	483 a	489 a	38.4 ab	31.5 bc	72 b	50 a	0.363 ab	2.7 a
				Joly				
Control	433 c	554 b	34.9 a	32.4 a	85 a	53 b	0.485 ab	4.6 a
CCC	496 bc	496 b	33.4 a	33.7 a	84 a	53 b	0.476 ab	4.1 a
3:1	536 b	724 a	32.6 a	22.5 b	86 a	63 a	0.417 bc	3.2 b
1:1	618 a	737 a	32.4 a	25.8 b	86 a	68 a	0.434 bc	3.3 b
1.3	493 bc	509 b	32.7 a	33.4 a	85 a	53 b	0.513 a	4.4 a
Ethephon	562 ab	723 a	33 0 a	23.3 b	85 a	64 a	0.403 c	3.2 b
				Laurier				
Control	503 cd	338 c	44.6 a	36.4 b	84 a	50 c	0.349 a	3.7 a
CCC	435 d	436 bc	41.9 ab	40.5 a	79 b	54 c	0.389 a	3.8 a
3:1	485 cd	543 ab	35.8 d	32.3 bc	75 b	67 a	0.355 a	3.6 a
1:1	555 bc	485 ab	40.3 bc	30.7 c	77 b	61 b	0.360 a	3.4 a
1:3	637 ab	599 a	39.0 bc	25.8 d	76 b	55 c	0.357 a	3.3 a
Ethephon	678 a	556 a	38.6 cd	28.0 cd	77 b	66 ab	0.371 a	3.8 a
				Leger				
Control	432 a	328 d	34.8 b	36.3 a	90 ab	52 a	0.498 a	4.5 a
CCC	420 a	387 cd	38.3 a	35.4 a	92 ab	50 a	0.475 ab	4.1 ab
3:1	504 a	460 bc	37.3 ab	28.1 bc	89 b	53 a	0.432 b	3.9 b
1:1	454 a	492 abc	36.6 ab	32.6 ab	93 a	50 a	0.472 ab	4.1 a
1:3	500 a	401 cd	38.3 a	32.3 ab	91 ab	52 a	0.428 b	4.1 ab
Ethephon	475 a	543 a	36.9 ab	26.2 c	93 a	53 a	0.481 ab	3.4 c
C.V.(%)	14.6	18.9	5.8	10.4	3.4	1.8	10.8	12.9

[‡] Lsmeans = means of spikes m^{-2} adjusted for the stand counts.

[†] Lsmeans or means of the same source (cultivar and PGR combination) within the same column followed by different letter are significantly different by a F-protected LSD ($p < 0.05$) analysis.

Table 7.2. Means of spikes m-2, grains/spike, 1000-grain weight and harvest index based on main culm (MC) or tiller culm (TC) as affected by cultivar and PGR combinations (1988)

Source	Spikes[1] m^{-2}		Grains per spike		1000-grain wt (g)		Harvest index	
	MC	TC	MC	TC	MC	TC	MC	TC
				Cadette				
Control	280[2] a	233 a	14 b	15 a	40.0 ab	16 1 f	0 364 b	0 187 a
CCC	287 a	215 a	23 a	11 a	39.5 ab	20.4 b	0 455 a	0 207 a
3:1	308 a	233 a	18 ab	12 a	40 1 ab	21 2 b	0.434 ab	0 217 a
1:1	284 a	233 a	22 a	13 a	39.9 ab	21 3 b	0 445 ab	0 241 a
1:3	307 a	175 a	18 ab	11 a	42.5 a	20 1 b	0 415 ab	0 167 a
Ethephon	262 a	222 a	19 a	14 a	38 4 b	20 7 b	0 412 ab	0 270 a
				Joly				
Control	344 a	220 c	24 a	13 b	37 1 a	18 6 a	0 526 a	0 319 b
CCC	290 a	205 c	25 a	12 b	38.0 a	19 5 a	0.515 ab	0 301 b
3.1	141 b	593 a	15 b	22 a	29.2 c	21 1 a	0 257 c	0 489 a
1:1	310 a	440 b	19 b	19 a	34 6 ab	19 2 a	0 436 b	0 427 a
1:3	344 a	170 c	28 a	14 b	36.7 ab	18.3 a	0 557 a	0 274 b
Ethephon	117 b	615 a	15 b	20 a	33.0 b	21 3 a	0 241 c	0 480 a
				Laurier				
Control	181 a	160 c	16 ab	12 b	45.6 ab	21 8 a	0 390 ab	0 238 c
CCC	235 a	195 bc	18 a	11 b	47 2 a	23 0 a	0 443 a	0 250 c
3:1	259 a	273 bc	13 bc	13 ab	44.4 ab	22.4 a	0 371 ab	0.326 bc
1:1	192 a	285 b	13 bc	15 ab	44.6 ab	23.2 a	0 344 b	0 372 ab
1:3	159 a	440 a	9 c	17 a	42.1 b	22 8 a	0 244 c	0 424 a
Ethephon	155 a	403 a	9 c	17 a	42.0 b	24 8 a	0 259 c	0 439 a
				Leger				
Control	288 a	43 c	28 a	10 b	37 7 a	18.8 a	0 507 a	0 168 c
CCC	274 a	108 c	29 a	11 b	37 9 a	20 9 a	0 525 a	0 216 bc
3 1	211 a	245 ab	27 a	20 a	36.3 a	19 2 a	0 448 a	0 404 a
1:1	318 a	175 ab	26 a	14 b	36 5 a	18.8 a	0 524 a	0 271 bc
1:3	257 a	135 bc	26 a	13 b	36.0 a	19 3 a	0 491 a	0 230 c
Ethephon	256 a	278 a	26 a	21 a	34 9 a	18 1 a	0 504 a	0 444 a
C.V.(%)	20.5	31.4	19 6	22.9	6.5	11 1	13 8	21 4

[1] Lsmeans = means of spikes m^{-2} adjusted for the stand counts

[2] Lsmeans or means of the same source (cultivar and PGR combination) within the same column followed by different are significantly different by a F-protected LSD ($p < 0.05$) analysis.

Table 7.3. Main effects of cultivars and PGR on variables in spring barley

Source	Grains per spike		Harvest index	Days to maturity		Grain yield (t ha^{-1})
	1987	1988	1987	1987	1988	1987
Cultivar	**	**	*	**	**	*
Cadette	26[+] b	16 c	0.568 a	90.8 a	86.8 a	6.0 ab
Joly	26 b	21 b	0.537 ab	88.0 b	86.3 a	5.7 b
Laurier	22 c	14 d	0.512 b	86.3 c	87.0 a	6.0 ab
Leger	30 a	24 a	0.533 ab	88.2 b	84.3 b	6.4 a
PGR	**	ns	**	*	**	ns
Control	27 ab	19	0.558 ab	87.8 b	83.9 d	6.0
CCC	28 a	19	0.564 a	88.1 ab	85.5 c	6.2
3:1	27 ab	18	0.520 bc	88.9 a	86.8 b	5.9
1:1	25 ab	19	0.538 ab	88.4 ab	86.6 b	5.9
1:3	26 ab	19	0.554 ab	88.3 ab	86.2 bc	6.4
Ethephon	24 b	18	0.490 c	89.0 a	87.8 a	5.8
C.V.(%)	21.4	15.0	11.1	1.5	8.1	14.2

ns Not significant at the 0.05 level of probability.

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

[+] Means of the same source (cultivar or PGR) within the same column followed by the same letter are not significantly different by a F-protected LSD ($p < 0.05$) analysis.

Preface to Section 8

Section 8 is the material contained in a manuscript by Ma and Smith (1991e) submitted to the Agronomy Journal. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table is presented at the end of the section.

Following the discussion of the effects of early and timely PGR application (late application of CCC inclusive) on barley physiology and yield production in the previous sections, the effect of post-anthesis application of ethephon on yield components and yield production is addressed in this section.

Section 8

POST-ANTHESIS APPLICATION OF ETHEPHON IN RELATION TO FACTORS CONTRIBUTING TO THE YIELD OF SPRING BARLEY

8.1 Abstract

Ethephon application after heading may enhance the yield production of small grain cereal crops such as barley (Hordeum vulgare L.), and whea- (Triticum aestivum L.) by altering grain filling processes. The objective of this study was to evaluate the effects of post-anthesis (1 week after heading) ethephon application on variables contributing to the grain yield of spring barley cultivars. A field experiment, with application of ethephon at three rates (0, 240, and 480 g a.i. ha^{-1}) to two barley cultivars, 'Cadette' and 'Leger', was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquat) in Quebec, Canada in 1988, 1989 and 1990. A post-anthesis application of ethephon extended the grain filling period by 1 to 3 d with variation among both cultivars and years. The 1000-grain weight of both cultivars significantly increased in all 3 years while no changes were found in the other yield components (spikes m^{-2} and grains $spike^{-1}$). Grain yield of Leger (conventional cultivar) was increased 5 to 12 % over unsprayed controls while Cadette (semidwarf cultivar) grain yield was either not significantly altered or reduced. These results indicate that under climatic conditions such as those prevalent in northeastern north America post-anthesis application of ethephon can potentially enhance grain fill and yield of spring barley.

8.2 Introduction

Ethylene, a naturally occurring plant hormone, affects numerous plant processes including fruit ripening, flowering, sex-expression, and vegetative growth (Wareing and Phillips, 1981). The development of ethephon (2-chloroethyl phosphonic acid), a synthetic plant growth regulator that releases ethylene slowly inside plant tissues through a pH-dependent reaction (Warner and Leopold, 1969), has greatly increased the commercial use of ethylene in agronomic and horticultural production. Ethylene inhibits the movement of auxin in stem tissues, thereby reducing auxin's ability to promote stem elongation (Sachs and Hachett, 1972). Many studies have shown that ethephon can reduce plant height and prevent lodging in a variety of species (Dahnous et al., 1982).

Ethephon has been widely tested and marketed in Europe for lodging control and yield enhancement in small grain cereal crops, such as barley (Hordeum vulgare L.), and wheat (Triticum aestivum L.), and recently has been registered for use in barley in some areas of North America (Wiersma et al., 1986). However, yield increases following ethephon treatment are not consistent (Paterson et al., 1983), which has restricted its large-scale use (Leary and Oplinger, 1983). Moreover, yield reduction due to ethephon treatment has been reported for spring barley, and winter barley (Paterson et al., 1983). For example, a four-year regional test in Scotland showed that ethephon significantly decreased the grain yield of winter and spring barley in 17 % of the trials where ethephon was applied. Seventy-two % of such treatments showed no significant change in grain yield (Paterson et

al., 1983). In Eastern Canada, Caldwell et al. (1988) demonstrated that there was no increase in spring barley yield due to ethephon treatment when lodging was minimal. Gaska and Oplinger (1988) in the United States also demonstrated that ethephon application to corn (Zea mays L.) resulted in inconsistent yield alteration. Recent studies by Moes and Stobbe (1991), and by Foster et al. (1991) indicated that, in West Canada, caution must be taken when use of ethephon to control lodging of spring barley since reduction in grain yields often occurred even with lodging.

For lodging control, the recommended timing for ethephon application is from Zadoks' (Zadoks et al., 1974) growth stages (ZGS) 37 to 45 (Caldwell et al., 1988; Thomas, 1982). Early application of ethephon has increased the number of spike-bearing tillers (Section 7), and decreased the number of grains per spike (Hill et al., 1982; Brown and Earley, 1973) with little effect on weight per grain or yield (Section 7). Grain yield differences among treatments must be attributable to differences in the three primary components of yield (Petr et al., 1988). Brown and Earley (1973) sprayed ethephon to winter wheat and spring oat shortly before or at heading and found that height and lodging were slightly reduced with either no effect on wheat yields or reductions in oat yield. In general, the number of spikes per unit area, and the number of grains per spike are established by anthesis (Petr et al., 1988). Application of ethephon after anthesis could only affect grain weight, by alteration of dry matter production or allocation of photosynthates to the grain. This hypothesis has not been tested. In northeastern China, dry and hot

winds (daily maximum air temperature $\geq 30^{o}C$, relative humidity$\leq$ 30 % and wind at equal to or greater than 3 m s^{-1}) frequently occur during the later period of winter wheat grain fill. These adverse climatic conditions substantially affect dry matter partitioning and grain yield. Recent studies demonstrated that application of ethephon shortly after heading could combat the stressful effects of dry and hot winds, and enhance the grain yield of winter wheat through a better photosynthate allocation, in regions where dry and hot winds are a potential hazard (Professor J. C. Zhang, personal communication). In some areas of North America spring barley grain fill proceeded normally under hot conditions and sometimes with drought. How the plant might respond to ethephon application after heading remained untested. This study was conducted to evaluate the effects of ethephon rates applied after anthesis (1-wk after heading) on grain yield and other agronomic variables of two contrasting spring barley cultivars.

8.3 MATERIALS AND METHODS

The study was conducted on Bearbrook clay soil (fine, mixed nonacid, mesic Humaquat) at the Agronomy Research Center, Macdonald College of McGill University, Quebec, Canada during the 1988, 1989, and 1990 crop seasons. Precipitation for May, June, and July was 47, 75, and 37 mm in 1988, 84, 100, and 37 mm in 1989, and 79, 116, and 104 mm in 1990. Average temperatures for these months were 15, 18, and $23^{o}C$ in 1988, 16, 19 and $22^{o}C$ in 1989, and 12, 19, and $21^{o}C$ in 1990. The previous crop for 1988 was alfalfa (Medicago sativa L.), for 1989 oat, and for

1990 barley. In each year, the land received 15-27-51 kg ha^{-1} of N-P-K fertilizer prior to seeding. In 1988, 1989 and 1990, 30, 100, and 100 kg N ha^{-1} respectively of ammonium nitrate were broadcast immediately after seeding.

The experimental design was a 2 x 3 factorial, arranged in a randomized complete block design with 4 replicates. Two barley cultivars, Cadette (a semidwarf lodging-resistant type) and Leger (a conventional, lodging-susceptible type) were treated with ethephon at a rate of 0, 240, or 480 g a.i. ha^{-1} one week after heading. Each plot was 3.8 m x 1.1 m, with 11 rows spaced 0.1 m apart. The growing season for spring barley in this region is very short, and tillering does not contribute much to yield. Thus, spring barley should be seeded at higher rates (Ma and Smith, 1991, unpublished result). In this study plots were seeded at 450 seeds m^{-2}, using a cone-type plot seeder on 3 May 1988, 1 May 1989, and 1 May 1990. In each year the crop density established was approximately 400 plants m^{-2}. Weeds were controlled with a mixture of 280 g a.i. ha^{-1} of bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) and 646 g a.i. ha^{-1} of diclofop-methyl (methyl 2 - (4- (2, 4 - dichlorophenoxy) phenoxy) proponate) at ZGS 12. Heading was recorded as the date when 50 % of the culms in a plot had spikes at least half exposed from the flag leaf sheaths. One week later ethephon was applied by using a backpack sprayer. The spray volume was 345 L ha^{-1}, at a pressure of 207 kPa. Citowett Plus (50 % alkylaryl polyglycol ether) at 0.05 % (v/v) was used as a surfactant.

Stand counts were made shortly after seedling emergence in a 1-m pre-marked section of row. Lodging scores (Oplinger et al., 1985)

were determined at ZGS 83 and again at 1 d prior to harvest. Lodging index for each plot was calculated as the average of these two readings. At crop maturity the previously marked 1-m section was hand harvested by cutting at ground level for determination of the number of spikes m^{-2}, number of grains per spike, and harvest index. A spike was counted if at least one fully-filled seed was present. Plants from the 1-m sample were air-dried at approximately 40°C for 10 d. The dried plants were weighed to determine the above-ground biomass, and threshed to determine the grain weight. Harvest index (HI) was determined dividing grain weight by above-ground biomass. Grain number was calculated from the total number of grains in the 1-m section divided by the total spike number of the same sample. The remainder of the plot (3.6 x 1.1 m) was combine harvested for yield determination. The combined plot yield was reported on a 0 g kg^{-1} moisture content (Moes and Stobbe, 1991). A subsample of the plot yield was taken for 1000-grain weight (TGW) determination.

In 1990 photosynthetic rates of the penultimate leaves were measured 10 d after ethephon application, with a Li-Cor LI-6200 portable photosynthesis system. The penultimate leaf was chosen, instead of the flag leaf, because of its longer and wider dimensions. Two reprensentive plants in each plot were randomly chosen and two photosynthesis readings were taken from each plant. The resulting photosynthetic measurements were covariate-adjusted for ambient light intensity, and CO_2 concentration, which were measured at the same time.

Data were analyzed with the SAS system (SAS Institute, 1985). For

each measurement, experimental error variances from each year were tested for homogeneity using Bartlett's test (Gomez and Gomez, 1984). Combined analysis of variance across years was performed and reported if the error variances were homogeneous. The F-test (Steel and Torrie, 1980) was used to determine whether the variations caused by treatments and their interactions were significant. Probabilities of less than or equal to 0.10 were considered significant for main effects and interactions. An F-protected $LSD_{0.05}$ was calculated to compare means of variables found to vary significantly. Although tillering could compensate differences in crop density due to uneven seeding it is probably unable to achieve complete compensation under short crop growing seasons (Ma and Smith, 1991, unpublished results). Therefore, stand count was used as a covariable to adjust for any effect of uneven seeding on yield components, and least square means of cultivar, ethephon rate and their combinations were presented if the covariable had a significant effect.

8.4 RESULTS AND DISCUSSION

In 1988, plant growth and development was markedly suppressed due to low precipitation and high temperature conditions prior to heading (Section 7). Average grain yields combined across all treatments were 2.6 Mg ha^{-1} in 1988, 6.7 Mg ha^{-1} in 1989, and 6.9 Mg ha^{-1} in 1990. Although the experimental error variances for all the variables measured were homogeneous across years, the combined analysis showed that there was a significant year x treatment interaction for most variables measured. For these reasons barley performance is discussed

for each year.

Plant performance A significant interaction between ethephon rate and cultivar for the number of days from seeding to maturity was observed in 1989 and 1990. In Cadette, application of ethephon at 240 g a.i. ha^{-1} significantly delayed maturity by 1.5 to 3 d. In Leger, ethephon at 480 g a.i. ha^{-1} also delayed maturity (1 to 3 d), while the lower rate showed little effect (Table 8.1).

In 1990, the penultimate leaf photosynthetic rate was increased more than 10 % by ethephon when measured 10 d after ethephon application (Table 8.2). Extension of the grain fill period and possible enhancement in photosynthetic rate (one year's data) indicate that ethephon treatment might have altered dry matter production.

As expected neither plant height nor lodging index was significantly affected by ethephon treatment (data not shown). This concurred with the findings of Dahnous et al. (1982) and Brown and Earley (1973), although their application times were earlier than this study.

Grain yields The combined analysis across years revealed a significant interaction of cultivar and ethephon rate for grain yield. Under the unfavorable weather conditions of 1988, application of ethephon at the higher rate (480 g a.i. ha^{-1}) decreased grain yield of Cadette, while Leger grain yield was not affected by ethephon application (Table 8.3). In 1989, with more normal rainfall during growing season, Leger grain yield was increased by 12 % at the 240 g

a.i. ha^{-1} rate and by 9 % at the 480 g ha^{-1} ethephon rate, while grain yield of Cadette was reduced 10 % at the higher ethephon rate (Table 8.3). A similar trend was observed in 1990; however, ethephon at 240 g a.i. ha^{-1} did not significantly increase Leger grain yield and there was no change in yield of Cadette due to ethephon application (Table 8.3).

The post-anthesis application of ethephon to spring barley at both 240 and 480 g a.i. ha^{-1} significantly influenced grain yield. There was a consistent interaction between ethephon rate and cultivar. The treatment nearly always favored grain production by Leger (conventional cultivar) while the grain yield of Cadette (semidwarf) was either not significantly altered or was reduced, indicating a differential cultivar sensitivity to ethephon. Although our application times were quite different from those of Caldwell et al. (1988) and Simmons et al. (1988), our conclusion agreed with theirs in that they noted that cultivar sensitivity to ethephon treatment (at ZGS 37 and /or ZGS 45) varied widely.

It has been demonstrated that ethephon is effective in reducing height and lodging in spring barley, winter barley and wheat (Dahnous et al., 1982; Wiesma et al., 1986; Simmons et al., 1988; Moes and Stobbe, 1991). However, the effect on yield is less clear with either increases only under lodging conditions (Cadwell et al., 1988) or substantial reductions even with lodging (Moes and Stobbe, 1991; Foster et al., 1991). Therefore, it is a significant finding that in this study ethephon application after anthesis increased grain yield. The increment in yield was probably due to a prolonged filling period

(Table 8.1), which allowed more photosynthate production. Dry matter partitioning may not be a contributing factor to the increased yield as harvest index was not altered by ethephon treatment in this study (data not shown). The 1989 yield increase at 240 g a.i. ha^{-1} of ethephon was not associated with extension of the time to maturity, which raised the doubt that extension in filling period was the only reason for the gain in the weight of grain. The increase in source strength by ethephon treatment (Table 8.2) might be an alternative explanation for the yield enhancement by ethephon treatment. Ethephon application may also have affected sink strength by alteration of dry matter deposition rate, resulting in higher grain weight. However, this possibility was not directly investigated in this study.

Thousand-grain weight Ethephon application increased 1000-grain weight (TGW) in all 3 years for both cultivars, in spite of the unfavorable effect of ethephon on Cadette yield. In 1988, the average TGW ranged from 36.9 g for the control treatment to 41.2 g for 480 g a.i. ha^{-1} ethephon rate. The increase in grain weight was greater at the higher rate of ethephon application (480 g a.i. ha^{-1}). Significant increases in TGW following ethephon treatment also occurred in 1989 and 1990, although the magnitudes were less than in 1988 (Table 8.4). These results disagree with Pearson et al. (1989), who reported that the effect of ethephon application on grain weight is negligible.

As with the effects on yield the grain weight gain could have been due to higher rates of photosynthetic production and photoassimilate

partitioning to the grain, or longer periods of grain fill, or both. In our study, ethephon significantly delayed maturity (Table 8.1), so that a longer filling period could have caused the gain in grain weight.

Ethephon treatment prior to heading usually shows little positive effect on grain weight and sometimes decreased it (Section 7; Moes and Stobbe, 1991). Thus, it is of interest that an increase in 1000-grain weight was observed in all 3 years of our study. In this study only one application time was tested. If the time of application was further refined, a consistent and larger enhancement in grain yield might result from late ethephon application. This might result in increases in Cadette grain yield. We found that early application of ethephon to spring barley, at ZGS 30, delayed maturity (Section 7). A greater number of tillers or spike-bearing tillers was associated with the earlier application, when tillers might have been released from the apical dominance due to change in the plant hormone balance by ethephon treatment. In the latter case delayed maturity resulting from ethephon application may alter the hormone allocation, such that grain production was favored. Cadette is a semi-dwarf cultivar. Its response to gibberellin and other regulators might differ from Leger, a taller cultivar, and its sensitivity to elongation and any related processes regulated by these hormones may be altered.

Spike number It was surprising that the number of spikes m^{-2} was significantly reduced in 1988 and 1990 by a late application of ethephon. It may be that many high-order tillers were sterilized by

the ethephon treatment. In triticale (X Triticosecale Wittmack), Sapra et al. (1974) has demonstrated that application of ethephon at high rates during the late boot stage increased male sterility. The reduction of the spike number by ethephon treatment was less severe in Leger than in Cadette, although the interaction effect on this variable was not significant ($P>0.1$, data not shown). A possible explanation for the difference between cultivars may lie in the later date of anthesis (2 to 3 d) for Cadette than for Leger (Section 3), although the difference in date of heading was only approximately 1 d (Agriculture Canada, Food Production and Inspection Branch, registration No. 2711 and No. 2237). During the early stages of grain formation, cells in the embryo and endosperm were vigorously dividing and differentiating, and the meristemic tissue may have been more sensitive to ethephon treatment than more developed tissues.

Grain number Ethephon treatment at either the low or the high rate did not significantly alter the number of grains per spike (Table 8.4). It should be noted that the number of grains per spike was substantially lower in 1988 than in 1989 or 1990. It seems probable that, in 1988, the below normal rainfall during the pre-heading stage caused this large difference.

Economic Effects In two out of the 3 years of this study, ethephon application (480 g a.i. ha^{-1}) increased grain yield by more than 8 %, or more than 0.5 Mg ha^{-1}. Assuming that constant prices were approximately Can$120 ($102 U.S.) Mg^{-1} of barley, Can$45 L^{-1} of

ethephon and Can$8 ($7 U.S.) for labor the yield increase represented a gross gain of Can$60 ($51 U.S.) ha^{-1}, or a net gain of Can$7 ($6 U.S.) ha^{-1} obtained from this measure. If the ethephon rate of 240 g a.i. ha^{-1} was as effective as the higher rate (as the 1989 data), a net gain of Can$30 ($26 U.S.) ha^{-1} would result.

In summary, this study has provided the following information about the response of yield components and grain yield of two currently produced spring barley cultivars, which are quite different in growth habit, when subjected to post-anthesis ethephon application: 1) post-anthesis application of ethephon at the conventional rate (480 g a.i. ha^{-1}) can increase spring barley yields in some cultivars when normal climatic conditions occur, 2) the primary component of such yield increment is enhanced 1000-grain weight, 3) generally post-anthesis application of ethephon does not affect the number of grains $spike^{-1}$. Although more extensive testing and analysis are required the data presented here suggest that post-anthesis application of ethephon may be useful for increasing the grain yield of at least some spring barley cultivars.

Table 8.1. The mean number of days from seeding to maturity as affected by ethephon rate in two spring barley cultivars in 1988, 1989, and 1990.

Cultivar	Ethephon rate (g a.i. ha^{-1})	Days from seeding to maturity		
		1988	1989	1990
		---------- No. ----------		
Cadette	0	92	89 b†	90 b
	240	92	91 a	93 a
	480	92	90 ab	92 a
Leger	0	86	86 b	89 b
	240	84	85 c	90 b
	480	85	87 a	92 a

† Means in the same column and within the same cultivar followed by different letters are significantly different by an F-protected LSD test.

Table 8.2. Photosynthetic rate (umol CO_2 s^{-1} m^{-2} leaf area) of penultimate blade at 10 d after ethephon treatment in 1990

Cultivar	Ethephon rate (g a.i. ha^{-1})	Photosynthetic rate (umol CO_2 s^{-1} m^{-2} leaf area)
Cadette	0	12.5†b
	240	14.5 a
	480	14.0 ab
Leger	0	17.6 b
	240	17.3 b
	480	19.6 a

† Least square means within the same cultivar followed by different letters are significantly different by an F-protected LSD test.

Table 8.3. Means of grain yield as affected by ethephon rate in two spring barley cultivars in 1988, 1989, and 1990.

Cultivar	Ethephon rate (g a.i.ha^{-1})	Grain yield		
		1988	1989	1990
		Mg ha^{-1}		
Cadette	0	2.43† a	7.23 a	6.94 a
	240	2.20 ab	7.22 a	7.27 a
	480	1.98 b	6.47 b	6.88 a
Leger	0	2.80 a	5.94 b	6.60 b
	240	2.83 a	6.68 a	6.88 ab
	480	3.15 a	6.51 a	7.13 a

† Yields are given at 0 g kg^{-1} moisture content. Means in the same column and within the same cultivar followed by different letters are significantly different by an F-protected LSD test.

Table 8.4. Least square means of spikes m^{-2} or grains $spike^{-1}$ and 1000-grain weight as affected by treatment main effect in 1988, 1989, and 1990

Source	Spikes m^{-2}			Grains $spike^{-1}$			1000-Grain weight (g)		
	1988	1989	1990	1988	1989	1990	1988	1989	1990
Cultivar									
Cadette	620† a	492	483	11.3 b	40.7 b	34.1	40.6 a	40.7 a	42.1 a
Leger	469 b	446	492	17.8 a	43.4 a	35.2	38.2 b	39.1 b	37.3 b
Ethephon rate (g a.i. ha^{-1})									
0	586 a	455	528 a	14.4	43.0	33.5	36.9 b	39.2 b	38.6 b
240	570 a	489	484 ab	13.3	42.5	34.4	40.1 a	40.0 ab	39.9 a
480	478 b	464	449 b	16.0	40.7	36.2	41.2 a	40.6 a	40.5 a

† Least square means or means in the same column and within the same source (cultivar or ethephon rate) followed by different letters are significantly different by an F-protected LSD test.

Preface to Section 9

Section 9 is the material contained in a manuscript by Ma and Smith (1991f) accepted for publication in the journal Crop Science. The format has been changed to conform as much as possible to a consistent format within this thesis. All literature cited in this section is listed in the reference section at the end of the thesis. Each table or figure is presented at the end of the section.

This section describes and evaluates a new method developed for delivery of substances (including PGR) into inflorescence of hollow-stemmed cereal grain crops.

Section 9

A NEW METHOD FOR SUPPLYING SUBSTANCES TO CEREAL INFLORESCENCES

9.1 Abstract

Study of nutritional and metabolic requirements of developing grain in cereal crops is hampered by the lack of methods for supplying substances directly to the spike over a substantial portion of the grain fill period. The objective of this study was to develop a system for continuous feeding of solutions containing nutrients or metabolic effectors into the peduncle of barley (Hordeum vulgare L. cv. Leger) plants and to observe their effects on the quantity and quality of the resulting grain. For each plant, one needle was inserted into the peduncle near the bottom and a second near the top. These were sealed to the peduncle with latex and attached to 20-cm lengths of flexible plastic tubing. The tubing on the lower needle was attached to a syringe barrel. Both the syringe barrel and the open end of the upper tube were held above the spike. Solutions were placed in the syringe barrel and these flowed through the peduncle and into the upper tube. The plants were allowed to draw solutions of N source (potassium nitrate or urea at 30 mM-N), or plant growth regulators (chlormequat at 5.8×10^{-3} mM or ethephon at 2.2×10^{-3} mM) from this system for 20 days. The volume of solution taken up ranged from 37 to 93 mL. Supplying these N sources with the peduncle perfusion system increased N concentrations in barley grain by up to 40 % and total grain N per spike by 25 % relative to nonperfused or distilled water perfused controls. The amount of N removed from the

perfusion system was equal to approximately 50 % of the total grain N per spike. Ethephon treatment also increased N concentration in barley grain. Use of the perfusion system was not disruptive the normal spike development. These results show that this peduncle perfusion system is capable of delivering large quantities of substances to the developing grain of hollow-stemmed grasses.

9.2 Introduction

Injection of radio-tracer solutions into hollow internodes of wheat (Triticum aestivum L.) culms is an effective way of studying carbohydrate metabolism in wheat reproductive structures because stem injection is less harmful to the plant than leaf blade feeding and because of more rapid movement of internode injected materials than leaf-fed materials into plant stem tissues (Brown and Neish, 1954). The explanation for this latter difference appears to lie in the relatively slow entry of leaf fed substances into the vascular system of the stem. Mature wheat plants retained a satisfactory level of carbon-14 following injection of ^{14}C-labeled sodium acetate into the lacuna of the upper internode of the growing plants (McConnell and Ramachandran, 1956). Using the same technique, McConnell and Finlayson (1967) injected ^{15}N-labeled ammonium chloride into the top internode of wheat plants and found that ^{15}N was readily incorporated into kernel components and that only negligible amounts of ^{15}N moved to the lower portions of the stem, below the injection point. Martin (1982) sprayed $^{15}NH_4{}^{15}NO_3$ onto leaf blades and sheaths of detached culms of wheat plants 22 d after anthesis; more than 50 % of the

absorbed ^{15}N was translocated to the spike within 24 h after application. The spike and the peduncle have a considerable in situ capacity to reduce and utilize nitrate immediately following anthesis so that $^{15}NO_3$ injected at this time is rapidly assimilated (MacKown and Van Sanford, 1986); however, in their experiment the amount of N injected represented only 5 % of total culm N at anthesis.

There are many advantages in using internode or peduncle injection techniques to monitor nutrient metabolism, assimilate partitioning and protein synthesis: nutrients can be added at specific times and in specific concentrations, assimilation is rapid, combinations of materials (nutrients, radio-labeled effectors, plant growth regulators) can be added and it is less damaging to the plant than leaf feeding. Restrictions, which limit the peduncle injection technique as a routine method for monitoring substance absorption, translocation, retranslocation and assimilation during the grain fill phase of small grain cereal crops, are the relatively small amount of solution administered to the peduncle in a single injection, the time consumed if repeated injections are made, and the risk of damage to the stem with repeated injections. A stem infusion technique to deliver methionine or boron into soybean (Glycine max [L.] Merrill) plants was successfully used by Grabau et al. (1986) and by Schon and Blevins (1987). The anatomy of cereal stem is different from that of soybean and other techniques can be applied. Because most grasses have hollow-stemmed internodes, introducing nutrients or metabolic effectors directly into cereal culms is feasible. Nitrogen is one of the most important and easily mobile macronutrients, and plant growth

regulators such as chlormequat and ethephon may alter dry matter partitioning during the grain fill (Section 6). They are, therefore, suitable for testing this technique. The objectives of this study were 1) to develop a system for continuous perfusion of nutrient or metabolic effector solutions into the peduncle of hollow-stemmed grasses for periods of weeks to months, and 2) to evaluate the effects of N sources and plant growth regulators delivered via this system on N and dry matter accumulation within the spike of barley (Hordeum vulgare L.).

9.3 Materials and Methods

Two experiments were carried out in the greenhouse of the Plant Science Department of McGill University, Ste. Anne de Bellevue, Quebec, Canada. The first experiment was planted January 17, 1990 and harvested on 30 April, 1990. The second experiment was planted April 2, 1990 and harvested on 30 June, 1990. The rooting medium was 4:1 mixture (by volume) of sandy loam soil and promix (containing 60 % peat moss, 20 % vermiculite and 20 % perlite). The plants were grown in pots that were 155 mm in diameter and 150 mm deep. Three seeds of a widely grown spring barley (cv. 'Leger') were planted in each pot. The seedlings were thinned to one per pot when the plants reached Zadoks growth stage (ZGS) 12, (when two leaves were unfolded) (Zadoks et al., 1974). The pots were examined daily, watered whenever necessary before plant heading, and watered twice daily thereafter. One hundred mL of 20-9-16.5 NPK commercial fertilizer (with chelated micronutrients) containing 600 mg N, 270 mg P, and 495 mg K per liter

of solution were added to each pot after thinning, and again at plant heading.

For each experiment, a large population of plants was established from which a smaller number was chosen for peduncle perfusion. A completely randomized design with 4 replicates was used for both experiments. Treatments consisted of nonperfused and distilled water perfused controls, plus two 30 mM N sources: potassium nitrate at concentration of 30 mM and urea at 15 mM, and two plant growth regulators: chlormequat (2-chloroethyl trimethylammonium chloride, CCC) at 5.8×10^{-3} mM and ethephon (2-chloroethyl phosphonic acid) at 2.2×10^{-3} mM. The concentration of the plant growth regulators (CCC and ethephon) were chosen to be such that in each case the total dose approximaterly equivalent to that received by field plants in a single application at the recommended rate for small grain cereals.

A syringe perfusion system was set up as shown in Fig. 9.1 when the plants reached ZGS 65 (anthesis). For each main stem, the flag leaf sheath was carefully opened to expose the peduncle for the maximum possible length without injury. Two 26-gauge needles were inserted into the peduncle at a 45^0 angle. The first needle was about 5 cm below the collar and served to allow air to escape during injection; the second needle was approximately 5-10 cm below the first and 2 to 10 cm above the flag leaf node. At the site of each needle injection, the peduncle surface and the needle were surrounded by a triangle of masking tape to form a cup against the side of the peduncle. The cup was filled with fluid latex (Vultex, General Latex Canada Inc. Candiac, Quebec), which dried overnight, sealing the needle to the

peduncle. Solutions were added to the system when the latex was completely dry (after about 24 h). Flexible plastic tubing (Tygon i.d. 0.8, o.d. 2.4 mm) was connected to the needles and fixed with silicone seal. These needles were the standard disposable type (Becton Dickinson and Company Rutherford, USA), with the plastic portion removed. A 20 mL syringe barrel fitted with a 21-gauge needle was attached to the tubing leading to the lower needle. This syringe acted as a reservoir of the solution to be tested and was held above the spike. The top of the syringe barrel was covered with aluminum foil to avoid loss of solution through evaporation and to prevent insects from falling into the reservoir. The open end of the other tube was held above the top of the syringe barrel. When solution was added to the syringe barrel, it flowed into the bottom of the peduncle, through the peduncle, and into the tube at the peduncle top. The level of the solution in the syringe barrel reservoir and the upper tube were always the same. The whole system was attached to a bamboo support stake with a rubber band. In each experiment, 1 or 2 of the 18 peduncles initially injected showed signs of leakage or blockage. This potential problem was easily dealt with by equipping more plants than were needed with the injection apparatus.

Approximately 20 d before main-stem spike ripening, treatments were imposed, on March 29 in the first experiment and June 4 in the second. After a solution was added to the syringe barrel, injected peduncles were examined at 1000h daily to make sure that solution was moving out of the syringe reservoir and that there were no leaks.

Date of maturity and number of aborted spikelets on the main-culm

spike were recorded. The spikes from each main-culm of the perfused and nonperfused plants were divided into 3 sections: bottom (starting from the lowest node of the rachis where at least one seed set was attached, to the 7^{th} node), middle (from the 8^{th} node to the 14^{th}), and top (from the 15^{th} node to the tip of the spike). On average there were 23 seed-bearing nodes per main-culm spike. The grains for each section were counted, oven-dried at $70^{0}C$ to constant weight, and weighed. Grains were ground with a Udy cyclone mill fitted with a 1 mm screen. The resulting flour samples were digested with sulfuric acid plus S-type Kjeltabs catalyst (Tecator Manual, Kjeltec System 1002 Distilling Unit) and the resulting ammonium was distilled into boric acid and quantified by titration with dilute acid (AACC, 1983; Bradstreet, 1965). Results were expressed as average weight per grain, and grain nitrogen concentration ($g\ kg^{-1}$).

The data were analyzed with two kinds of ANOVA procedures using the SAS package (SAS Inc., 1985), according to Steel and Torrie (1980): 1) ANOVA based on a compeletely randomized design, and 2) ANOVA based on a split plot design, where the section of the spike was taken as a subplot, and the treatment was the whole plot. The amount of solution delivered into a peduncle was used as a covariable for the analysis of average grain weight and grain nitrogen concentration. Significance between individual means or least square means was determined by a protected LSD (P=0.05) analysis. Results were reported either in pooled form, if error mean squares of both experiments were homogenous, or separately if heterogenous, as determined by Bartlett's test (Steel and Torrie, 1980).

9.4 Results and Discussion

Both experiments showed that continuous feeding through the peduncle perfusion system (PPS) described here is an acceptable method for studying the metabolism of nutrients or possibly metabolism modifying substances during the grain filling period. The volume of solution administered over the 20-day feeding period into the peduncle averaged 35 mL per peduncle in the first experiment (when the climate was relatively cooler) and 63 mL per peduncle in the second experiment. Table 9.1 shows the means $\pm$ standard deviations of solution absorbed and the total amount of grain N per spike for each treatment. Variations in volume of solution absorbed via the peduncles ranged from 31 to 46 mL in experiment 1, and 37 to 93 mL in experiment 2. The wide range in uptake levels could be dealt with by using level of uptake as a covariable; controlling feeding period length for exact amount of perfused nutrient added to each plant; or increasing sample size in future experiments. For each plant, lowering the open end of the upper tube to the level of the peduncle resulted in solution dripping from that tube at a rate of several mL per minute. This indicates that the variation between plants in rate of solution uptake was not due to restrictions on the rate of solution delivery to the peduncle, but rather to differences in solution absorption between plants. In these experiments the volume of solution absorbed was not a significant covariable for average grain weight and grain N concentration. Differences in the amount of perfused N solution and distilled water uptake are probably due to more negative osmotic

potential of the perfused N solution than the perfused water.

Peduncle perfusion with N solutions increased grain N per spike 20 to 40 % relative to that of nonperfused or perfused with distilled water controls (Table 9.1). These increases in grain N per spike represent 30 to 60 % of the total N that was absorbed from the perfusion system by the plants. Because plants receiving N from the perfusion system may acquire less N by root absorption than controls, this difference calculation represents a minimal estimate of the concentration of N from the perfusion system to grain N accumulation. The total amount of N absorbed from the perfusion system was generally equal to about 50 % of the total spike N. Plants taking up the highest volumes of perfused N containing solutions took up N equivalent to 100 % of the total spike N (data not included). The fate of this N was not determined in this study. In this initial testing of the system we have been conservative with regard to the concentrations of N in the perfused solutions. As there was no evidence of osmotic injury to any of the perfused plant tissues it seems likely that higher concentrations will allow uptake of higher amounts of N without damage to the plants.

A number of publications have reported studies of metabolism and retransloction of N or other mineral nutrients during the grain fill phase, through use of spike culture techniques (Corke and Atsmon, 1988), peduncle injection (MacKown and Van Sanford, 1986), tissue culture (Barlow et al., 1983; and Singh and Jenner, 1983; Chen and Hayes, 1989), or through periodic sampling under greenhouse conditions (Dalling et al., 1975; and Dalling et al., 1976; Corke et al., 1989).

It is proposed that our current system is simpler and/or more efficient than these methods.

Using the technique described here the amount of solution injected into the peduncle and the length of time available for plant uptake of the added solutions were both large. These conditions will allow various studies on: 1) a wide range of plant nutrients, with additions made through solutions of constant or changing concentrations; 2) plant growth regulators (PGRs) or plant hormones; 3) fungal and bacterial toxins; 4) carbohydrates, organic acids, amino acids and other organic metabolites; 5) isotope studies, with isotopes added alone or in the presence of other nutrients, PGRs, etc. This method represents a modification of simple syringe injection into the hollow stem (McConnell and Finlayson, 1967; McConnell and Ramachandran, 1957) or peduncle (MacKown and Van Sanford, 1986) of small grain cereals. This method has some similarities with the stem infusion technique used on soybean (Glycine max [L.] Merrill) (Grabau et al., 1986), but takes advantage of, and is more suitable to the anatomy of hollow-stemmed grasses. In all cases where simple injection was used to add substances to cereal plants, aqueous solutions administered to the plants were only 0.1 to 0.2 mL per injection. Previous peduncle injection experiments were able to supply amounts of N that were only a small fraction of the total N in the spike. For instance, MacKown and Van Sanford (1986) supplied 5 % of the total spike N by injection into the peduncle. With the PPS described here the amount of N delivered into peduncle was much higher than previously reported (Table 9.1). With this system, up to 70 mL solution was absorbed

through the barley peduncle in the 20-d period.

Under well-watered greenhouse conditions, average grain weight was quite high (40 mg), while grain N concentration was relatively low, only 18.6 g kg^{-1} for both plants that were not perfused or those that were perfused with water (Table 9.2). Peduncle perfusion with KNO_3 and urea significantly increased grain N concentration without substantially affecting grain weight. The concentration of N in grain was 22 to 24 % (experiment 1) respectively, and 31 to 40 % (experiment 2) respectively higher in plants fed N as KNO_3 or urea, than in nonperfused control plants (derived from Table 9.2); a similar result was evident when the comparison was with plants perfused with distilled water. In experiment 2, the water-perfused control was slightly higher in grain N concentration than that of nonperfused plants. Through use of the spike culture technique, Corke and Atsmon (1988) showed that in barley grain, very high protein concentrations can be achieved under high N (280 mM) conditions. They measured barley kernel protein concentrations of up to 350 g kg^{-1} dry weight. However, seed weight was not reported in their paper. It may be that their treatments resulted in normal production of seed protein with substandard levels of starch accumulation and little actual increase in the absolute amount of total spike grain protein. This will produce a high percentage of grain protein that is not due to an increased deposition of protein in grain. Our treatments did not produce N concentration values as high as those of Corke and Atsmon (1988), however we measured grain (including lemma and palea) instead of kernel N concentration, and the concentration of N solutions used

in our experiment was cautiously low. Different rates of N injection and various periods of feeding will be investigated.

Ethephon, when applied at ZGS 39 to 45, at 480 g a.i. ha^{-1}, may increase grain protein by 0.5 to 1 % under field conditions (our unpublished results). This effect was also shown to result from perfusion of ethephon in one of the experiments, while chlormequat perfusion did not alter grain N concentration (Table 2).

A dominance hierarchy existed among spikelets of a spike rachis, with the central spikelets developing first and producing the largest seeds. The treatments used in these experiments did not change this. This gradient was probably established during early apical development, prior to application of the perfusion treatments. The rank for grain weight was middle > bottom > top, and bottom > middle = top section of the spike for grain N concentration (Table 3).

There were no differences in spike number per plant, aborted spikelets per mainculm spike, grain set per mainculm spike or date of maturity due to the applied treatments (data not shown). In addition, no necrosis or lesions were seen on peduncles being perfused. These observations indicate that the PPS described here is not stressful to the culm or disruptive to normal spike development.

Fig. 9.1. Illustration of setup of the perfused solution via peduncle of barley main-culm.

Table 9.1. Absorption of perfused solution (mL) through the peduncle and the total grain N per spike.

Values are mean of 4 plants ± SD for four treatments

Treatment	Perfused solution		Total grain N per spike	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
	---------- mL ----------		--------- mg ---------	
KNO_3	37.5±5.8	37.0±4.8	55.5±2.4	60.4±8.2
Urea	46.0±8.0	42.8±21.0	56.6±5.1	63.1±12.6
Chlormequat	36.5±10.3	74.5±33.5	51.5±2.1	54.9±10.3
Ethephon	31.5±8.7	93.0±57.8	45.9±3.2	54.0±9.7
Distilled H_2O	45.8±4.8	68.3±32.3	47.6±1.7	46.2±8.6
Control	0	0	45.8±1.5	43.7±9.8

Table 9.2. Means of average grain weight and grain N concentration. (averaged over replicates on all grains of fed spikes)

Treatment	Grain weight		Grain N concentration	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
	--- mg/grain ---		---- g kg^{-1} ----	
KNO_3	34.0	42.9	23.2† a	23.5 ab
Urea	38.5	38.5	22.9 a	25.1 a
Chlormequat	39.1	41.8	20.0 b	19.9 cd
Ethephon	39.5	39.9	18.1 c	21.8 bc
Distilled H_2O	38.3	41.1	18.6 bc	20.8 c
Control	37.8	42.6	18.7 bc	17.9 d
Difference‡	NS	NS	***	***

† Means followed in the same column by different letters are significantly different by a protected LSD (P=0.05) test.

‡ NS, or *, *** No significant differences or differences significant at the 0.05, 0.001 level of probability, respectively.

Table 9.3. Means of grain weight (MGW) (mg), grain percent protein (GPP), and total protein per grain (TPG) (ug) for each section of the spike (averaged over replicates)

Section of spike	Grain weight		Grain N Concentration	
	Exp 1	Exp 2	Exp 1	Exp 2
	--- mg/grain ---		---- g kg^{-1} ----	
First 7 nodes	41.2[+]b	43.2 b	20.5	22.3 a
Second 7 nodes	43.5 a	47.4 a	20.0	21.0 b
Top nodes	36.5 c	40.6 c	20.2	21.3 b
Difference	***	***	NS	***

[+] Means followed in the same colum by different letters are significantly different by a protected LSD ($P < 0.05$) test.
NS, or *** No significant differences or differences significant at the 0.001 level of probability, respectively.

Section 10

GENERAL DISCUSSION

10.1 Apex Development

The timing of developmental events in spring barley is strongly influenced by climatic and cultural conditions. Under North Eastern North American continental climatic field conditions we found that the main-stem apices of spring barley reached the double ridge stage at 22 to 24 DAS, or at 320 to 340 AGDD. The lemma primordium was normally initiated about 29 to 32 DAS (450 to 470 AGDD). Awn initiation occurred when the number of primordia reached its maximum value, approximately 40 to 44 DAS (650 to 680 AGDD). Anthesis occurred about 53 DAS (860 AGDD) for Leger and 56 DAS (940 AGDD) for Cadette. Variations in the timing of apical development stages were greatly reduced, but were not removed when the data were related to AGDD. The differences that remained were probably attributable to the below normal precipitation in 1988 which may have accelerated apex development. In two-rowed barley, Kirby and Faris (1970) demonstrated that the double ridge stage occurred earlier under higher plant densities than under lower or normal densities. Severe water or nutrient deficiencies were reported to affect spikelet initiation rate in wheat (Holmes, 1973; Purvis, 1934), and barley (Nicholls and May, 1963). Recently, Frank (1988) reported that increasing the N concentration in the rooting medium shortened the time required to reach each stage of spring barley apex development. Our results also

showed that temperature was not the only factor driving this process.

In Quebec, the apical development of spring barley is compressed into a relatively short period. We found that the entire process, from seeding to anthesis, took approximately 55 d (860 to 940 AGDD) under field conditions, and that approximately 30 d elapsed between the double ridge and anthesis stages (Table 3.2). Our observations differ from European data (e.g. Russell et al., 1982; Kirby and Appleyard, 1981; Kirby and Faris, 1970), where the apical development of spring barley lasts 10 to 20 d longer. The European growing season is cooler and longer than that of north-eastern North America, where the climate is generally continental. Thus, our data are more applicable to barley grown under North American continental conditions.

10.2 Primordia Production

Primordia consist of initials of leaves or spikelets. The initiation rates of these two were clearly in distinct phases. Assuming that 3 to 4 leaf primordia are already present in the mature barley grain (Kirby and Appleyard, 1981; Bonnett, 1966), by approximately 16 DAS, when sampling commenced, both Leger and Cadette had initiated all leaf primordia (in most cases 9 leaves were ultimately formed on the main shoot) and had 1 fully expanded leaf with another 1 or 2 visible leaves. The leaf primordia formed at a rate of 0.3 - 0.4 primordia d^{-1}. Under European field conditions Baker and Gallagher (1983) found that the transition from leaf to spikelet initiation was marked by an increased initiation rate, and commented that for cereals the increase

in rate represented the beginning of the reproductive phase, rather than the appearance of double ridges. This rate change occurred soon after production of the last leaf initial primordium (16 DAS in this study). At this time, the apex is in transition from the vegetative (producing initials of leaves, tillers and internodes) to the reproductive (initiating embryonic inflorescence) phase. From 16 DAS until lemma initial formation, approximately 30 primordia were produced in a second 16-d period, at an average rate of 1.9 primordia d^{-1} (Fig. 3.1). This phase was accompanied by the formation of spikelet organs. Thereafter, the primordium initiation was slowed, and eventually ceased at about awn initiation (approximately 40 DAS). This was followed by a reduction in primordium number due to the abortion of some tip primordia between the awn initiation and anthesis stages. These observations generally agreed with those of Kirby and Appleyard (1981), although our data indicate a higher rate of initiation, and a shorter duration of each phase. Presumably this is due to the differences between the climatic conditions in North American and those of Europe and possibly some differences between the barley cultivars grown in these regions.

10.3 Apical Development Stage in Relation to Morphological Traits

Understanding the impact of climate change on the processes of apical development allows accurate recommendations regarding the application of agrochemicals such as hormone-type herbicides or growth regulators. In this study we found that apical development of spring barley did not always keep pace with external vegetative growth stages such as

early ZGS. For instance, in 1988, there was hot weather and below normal rainfall early in the season (Table 3.1), which shortened the time required for the main-stem apex to reach specific stages (Table 3.2). The external morphology was less affected by the hot, dry conditions. When the 3rd leaf was fully expanded, i.e. Zadoks' growth stage (ZGS) 13, in most developed plants the main-stem apex was at the double ridge stage in 1987, and at the lemma initial stage in 1988. These observations agree with Cartwright et al. (1985), who claimed that no relationship existed between apex stage and ZGS in the early stages of plant development. This phenomenon partially explains the different responses of barley plants to PGR applications, in different experiments or in different years, even though PGR were applied at the same ZGS. Thus the development of the apex and therefore the components of grain yield, are differentially affected by climatic and managerial variation. This means that growth stages based on vegetative development (leaf, tiller or internode numbers) reflect apex development only very generally. Efforts to alter the development of yield components by the application of inputs such as PGR or N fertilizer side-dress cannot be accurately guided by vegetative development.

10.4 Plant Growth Regulators on Apical Development

The results presented in Section 4 indicate that the apical development of spring barley was transiently suppressed by the application of chlormequat at ZGS 13, in most cases, and at ZGS 30 in some cases. The effect of ethephon, applied at ZGS 13, on apical

development depended upon environmental conditions. The results showed that cultivars may respond to PGR in different ways. For Cadette, for example, both chlormequat and ethephon significantly retarded main-stem apical development when applied at ZGS 13, while for Leger, a significant retarding effect by early ethephon treatment was not observable until several days later after application (Tables 4.1, 4.2 & 4.3). In England, Waddington and Cartwright (1988) demonstrated that application of mepiquat chloride had a similar retarding effect on the main-stem apical development and growth of spring barley when applied at the lemma initial stage. The inhibition effects of the PGR treatment on main-stem apical development - reducing apical dominance - at early growth stages may aid in the tip spikelet development within the main shoot and tiller production within the plant, since more assimilates could become available for tiller initiation and growth. This probably is the basis for the changes in the tillering pattern, tillering dynamics, dry matter allocation, yield components, and final grain following PGR application. Reduction in tip abortion was observed (Table 4.4), but this was not reflected in the final grain number per spike. In fact, ethephon application often decreased the number of grains per spike (Table 6.3). It may be that ethephon retarded the development of the main stem apex shortly after flag leaf emergence (Table 4.4), and that at the time of heading (when observation on tip abortion was made), tip abortion just started and was not yet complete. Thus ethephon treatment only delayed tip abortion. Investigation into the mechanisms by which PGR alter the relationship between tip abortion

and final grain number could be done by serial sampling. This merits further investigation.

10.5 Plant Growth Regulator Effects on Tillering Pattern

Previous studies on the early application of CCC to winter or spring barley (before ZGS 30) did not show genotypic differences (Koranteng and Matthews, 1982; Williams et al., 1982; Matthews et al., 1981). With timely application of ethephon (ZGS 37 to 45) for lodging control Caldwell et al. (1988) demonstrated that different cultivars had different sensitivities to PGR treatment in terms of grain production and plant characteristics (reducing height and lodging). The results presented in Section 5 demonstrated that for tiller production Leger, the standard tall cultivar, was more responsive to the early CCC or ethephon treatment than was Cadette, a semi-drawf cultivar (Tables 5.1, 5.5).

In this study, we found early application of ethephon, at ZGS 30, (Tables 5.4, 5.6) or CCC, at ZGS 13, (Table 5.4) increased the number of shoots m^{-2} produced during the tillering phase. This resulted in a larger number of spike-bearing shoots m^{-2}, through an enhancement of tiller production rather than tiller survival (Table 5.4). As early application of growth retardant transiently suppressed growth and development of the main shoot, it seems that more assimilates are available for tiller bud initiation and their subsequent growth and development. Cartwright and Jaddoa (1985) concluded that a tiller must reach a critical developmental stage before main culm heading if it is to survive and produce grain. Matthews et al. (1981)

demonstrated that CCC treatment induced tillers to occur earlier. Early application of PGR probably promoted the development rate, tillers initiated earlier and the production of more tillers. Thus more tillers were produced but the final proportion of spike-bearing tillers (determined by their size at plant heading) over the maximum tiller number was similar to control plants. The control plants produced a smaller number of tillers but more of these survived to produce heads. Naylor et al. (1987) reviewed literature illustrating that CCC applied before ZGS 30 appears to reduce the sink capacity of the main stems, thereby freeing assimilates to contribute the growth of other parts of the plant, such as roots and tillers. This implies that more tillers could be produced as the dominance of the main-stem was reduced by the treatments. Late application of CCC (ZGS 39) or timely application of ethephon (ZGS 39) improved the production of spike-bearing shoots by increasing the proportion of already existing tillers that produced productive spikes, that is, tiller survival. This confirmed the findings of Simmons et al. (1988). Ethephon applied to the crop at ZGS 39 was added for lodging control; by ZGS 39 most of the tillers had already emerged and modification of spike numbers was only possible by enhancing tiller survival.

It should be noted that growing seasons for spring barley in Quebec are much shorter than those under which earlier European studies were conducted (Waddington and Cartwright, 1986; Koranteng and Matthews, 1982; Matthews et al., 1981). Under Quebec climatic and cultural conditions we found much less tillering than was reported in the European studies, so that tillers contributed relatively less to

grain yield in Quebec, particularly with hot and dry climatic conditions (Table 3.1), than in Europe. For instance, 2 to 3 spike-bearing shoots per plant were normally produced in European spring barley when produced under high plant densities, while under similar densities in Quebec spring barley plants produced only 1 to 1.5 spikes per plant, even with the application of PGR. A recent study by Foster et al. (1991) in Western Canada also illustrated that late tillering induced by ethephon application did not improve the yield potential under Western Canadian semi-arid conditions.

10.6 Yield Components and Grain Yield

Few previous studies had addressed early ethephon application to cereal crop tillering, instead, CCC treatments were often studied in this regard (see Naylor, 1987 for references). In this study we found that tiller production was more responsive to ethephon than CCC. Early application of ethephon alone or in combination with CCC is effective in promoting tiller production but does not improve grain production (Section 7).

It was surprising that post-anthesis ethephon application (ZGS 65) decreased the number of spikes m^{-2} (Section 8). It may be that many high-order tillers were sterilized due to ethephon treatment. In triticale (X Triticosecale Wittmack), Sapra et al. (1974) has demonstrated that application of ethephon at high rates during the late-boot stage increased male sterility. The reduction of the spike number by ethephon treatment was less severe in Leger than in Cadette (Table 8.3). A possible explanation for the difference between

cultivars may lie in the later date of anthesis (2 to 3 d) for Cadette than for Leger (Table 3.1), although the difference in date of heading was only approximately 1 d. During the early stages of grain formation, cells in the embryo and endosperm are vigorously dividing and differentiating, and the meristemic tissue should have been more sensitive to ethephon treatment than the more developed tissues.

The number of grains per spike was affected either positively or negatively by PGR treatment. CCC treatment usually affected (increased or decreased) this variable through changes in tiller shoots, while ethephon applied at ZGS 30 or 39 tended to reduce the number of grains per spike largely in MC's. This reduction contributed most to the reduction in grain yields for Cadette in both 1989 and 1990 (Table 6.6). When applied after plant anthesis ethephon at either the half or the normal rate did not significantly alter the number of grains per spike (Table 8.3).

In general, 1000-grain weight was little affected (Table 6.3) or occasionally increased by CCC treatment (table 7.4). In contrast, ethephon treatment prior to heading usually had little positive effect on grain weight and sometimes decreased it (Tables 6.3, 7.2). These findings were very different from some previously reported data (Green, 1986; Harris, 1984) but similar to the more recent studies of Moes and Stobbe (1991c) and Simmons et al. (1988). On the other hand, the major effect of post-anthesis ethephon application was a change in 1000-grain weight. This was true in both Leger and Cadette. However, the final result was a yield increase for Leger but a yield decrease or no change for Cadette.

Attempts to explain the effects of PGR on yield in terms of effects on yield components were complicated by the fact that over years there was no consistent response of any component to PGR treatments. The conditions (temperature and moisture) at the time of and immediately after PGR application may have influenced the rate of absorption and thus the response of yield to these PGR (Simmons et al., 1988). Or, differences in the stage of apical development at the time of PGR application (based on ZGS) may have resulted in differential responses to PGR. Further, a separation of spikes into main- and tiller-culms revealed that the interaction of PGR treatment by application stage on MC spikes was quite different from that on TC spikes, though the pattern of significance was similar (Table 6.4). Our data clearly indicated that application of CCC did not markedly affect any of the yield components in the TC's, while ethephon generally increased these variables in TC's. Increments in the yield components of TC's were partially or completely compensated for by reductions in these components in MC's. Since the MC spike was the major component contributing to grain yield per plant or per ha, the overall effect of ethephon applied at ZGS 30 or ZGS 39 on yield components was a reduction in the grain yield in 1989 and 1990, especially in the case of Cadette.

We found that in all situations - PGR application for lodging control (Section 6), early application of ethephon alone or in combination with CCC to promote spike-bearing shoots (Section 7), and post-anthesis ethephon application to monitor grain mass for yield production (Section 8) - there were always differential cultivar

sensitivities to the PGR treatment in terms of grain yield.

In general, ethephon applied at the recommended rate and application stage for lodging control either did not improve or deceased grain yield. This is contrary to the findings of Dahnous et al. (1982), and Caldwell et al. (1988), but agrees with the recent reports of Moes and Stobbe (1991a), and Foster (1991) in Western Canada. It should be noted that the work of Dahnous et al. (1982) was conducted at Pullman of Washington and ethephon was applied at late 'boot' stage, and the work of Caldwell et al. (1988) was conducted in Nova Scotia of Canada. In both cases the climatic conditions are humid and essentially maritime.

It should also be noted that control plots yielded well under lodging conditions in both 1989 (slight lodging) and 1990 (severe lodging). The real yield would probably have been much less under field scale production with comparable lodging conditions as lodged barley plants were harvested at a much lower height and with more care than would be possible for a commercial farmer. Ethephon applied at ZGS 39 was effective in lodging control (Table 6.7) for the tall cultivar Leger. Grain yield was, however, reduced by more than 27 % under the less severe lodging conditions of 1989. Similar to the recent findings of Moes and Stobbe (1991a), reductions in grain yield of ethephon treated plots were primarily due to reductions in grains per spike, particularly in the main shoot (Table 6.6). Therefore, caution must be taken when using ethephon as a practical measure for lodging control under continental climatic conditions such as those under which this study was conducted. Chlormequat, on the other hand,

did not prevent plant lodging, but often increased grain yield. Both PGR had a suppression effect on the main culm apices (Section 4). Ethephon treatment showed prolonged effects on main culms, which probably led to some MC spikes developing much behind the control plants. In extreme cases the MC was abolished completely; CCC temporarily retarded MC apices at earlier stages of apical development. The apices caught up later, near heading, which might have aided in the development of the primary tillers and the tip spikelets of the MC spikes. The number of MC spikes per unit land area was significantly reduced by ethephon, but not by CCC, which might explain the variation of grain yield effects following application of these PGR.

The post-anthesis application of ethephon to spring barley at both 240 and 480 g a.i. ha^{-1} significantly influenced grain yield (Section 8). There was a consistent interaction between ethephon rate and cultivar. The treatment always favored grain production by Leger, a standard cultivar, while the grain yield of Cadette was either not significantly altered, or was reduced. Different cultivars seem to have very different sensitivities to ethephon treatment. Though the application times were quite different, our conclusion agreed with Caldwell et al. (1988), who noted that cultivar sensitivity to ethephon treatment (at ZGS 37 and /or ZGS 45) varied widely.

10.7 Maturity, Plant Height and Lodging

Barley plants in ethephon-treated plots tended to be delayed in maturity compared to those untreated plots. This effect seemed to be

most evident when ethephon applied at ZGS 39. In contrast, application of CCC, although significantly delaying apical development when applied at an early growth stage, only slightly delayed plant heading with no observable effect on date of maturity (Table 6.6). These data agreed with Moes and Stobbe (1991a) for ethephon, but disagreed with Green (1986) for CCC, who stated that application of CCC to spring barley can extend the period of grain fill.

Plant height was significantly reduced by PGR treatment. There was a significant interaction of PGR with application stage within cultivar each year. Application of ethephon at ZGS 30 or ZGS 39 decreased plant height by 9 to 21 cm for Cadette in both 1989 and 1990, and by 5 to 32 cm for Leger each year (Table 6.7). In 1989, application of CCC to Cadette at ZGS 30 or ZGS 39 and to Leger at all application stages also significantly reduced plant height. However, the standing ability was improved only by ethephon applied at ZGS 39 for the standard tall cultivar, Leger. Early application of ethephon, at ZGS 13 or ZGS 30, and application of CCC at ZGS 30 slightly, yet significantly increased lodging in Cadette, a semi-drawf cultivar, under the severe lodging conditions of 1990. These results agree with those previously reported (Simmons et al., 1988; Dahnous et al., 1982). It is easy to understand why post-anthesis (ZGS 65) ethephon application did not affect plant height or lodging since by the time of application the vegetative parts had been already established.

10.8 Methodology

For studying the mechanism of N and other growth effectors, solutions

of effective substances have usually drenched into the soil or sprayed onto the surface of plant leaves. In both cases the exact amount of substance taken by plants would only be estimated, while the concentration was limited by the fact that leaves are very sensitive to high osmotic concentrations or toxins For plants with hollow internodes stem or peduncle injection can overcome the above limitation, however, the restrictions discussed in Section 9 limits the injection technique as a routine method for monitoring substance metabolism during grain fill phase. A peduncle perfusion system for delivery substances to cereal crops has been successfully developed in this study. Using our technique the amount of solution injected into the peduncle and the length of time available for plant uptake of the added solutions were both large. With this system, up to 90 mL solution was absorbed through the barley peduncle in a 20-d period. These conditions will allow various studies on: 1) a wide range of plant nutrients, with additions made with solutions of constant or changing concentrations; 2) plant growth regulators (PGRs) or plant hormones; 3) fungal and bacterial toxins; 4) carbohydrates, organic acids, amino acids and other organic metabolites; 5) isotope studies, with isotopes added alone or in the presence of other nutrients, PGRs, etc.

Section 11

SUMMARY AND CONCLUSIONS

The overall objectives of this work focused on the following four major aspects: (i) illustrating the apical development of spring barley under Quebec field conditions; (ii) evaluating the effects of CCC and ethephon timing on spring barley main-stem apical development; (iii) determining the subsequent impact of CCC or ethephon induced-inhibition of the main sink (main shoots or main spikelets within a spike) on tillering, formation of yield components and production of grain yield; in addition (iv) developing a system for delivery of various substances into developing cereal crop inflorescences. The following summary and conclusions completely satisfy our initial hypotheses.

It is well known that climatic factors strongly affect the apical development of cereal crops. In this study, the time and duration of key stages of apical development in spring barley were illustrated under North American continental climatic field conditions, and the thermal time requirement to reach these stages was determined. Apical development and primordium production are better related to thermal time than time alone, and apical development occurs more rapidly under the conditions in which this research was conducted than under those in which previously reported field work was carried out.

Application of PGR to cereal crops has a large impact on apical development. Early application of chlormequat, at ZGS 13,

significantly delayed the development of spring barley main-stem apices. The number of aborted spikelet primordia was significantly reduced by a ZGS 13 chlormequat application, probably because differences among spikelets within a spike for rate of development were minimized. Unlike chlormequat, application of ethephon did not immediately retard the main-stem apex. However, a retarding effect of ethephon was obvious a few days after application. Apical development was not tightly coupled with external morphological development (e.g. ZGS), which may explain the variable effects of PGR application on final grain yield.

Our results demonstrated that both genetic and climatic factors affected the response of barley plants to the application of PGR. Early application of ethephon alone or ethephon in combination with CCC, at the beginning of stem elongation is effective in increasing the number of spikes m^{-2}, through an increment in spike-bearing tillers in some cultivars, but does not increase grain yield. Plants treated with an early application of CCC (ZGS 13) or ethephon (ZGS 30) produced greater numbers of shoots, which appeared later in time, than control plants. The number of spike-bearing shoots was increased by early PGR treatment, primarily by enhancement of tiller number rather than tiller survival. Late application of CCC (ZGS 39) or application of ethephon at ZGS 39 when most of the tillers had emerged resulted in a higher number of spike-bearing shoots, mostly through increased tiller survival.

We found that early application of ethephon alone or in combination with CCC, at ZGS 30, often increased the number of spikes

m^{-2} while CCC applied at ZGS 13 enhanced the number of grains per spike, and early application of either PGR occasionally increased grain yield. In general, CCC showed fewer detrimental side effects on the barley cultivars tested than did ethephon. Plant height and lodging was reduced by ethephon applied at ZGS 39. However, this sometimes reduced grain yields due to the severe suppression of MC spikes.

It is quite interesting that post-anthesis application of ethephon at the conventional rate (480 g a.i. ha^{-1}) can increase spring barley yields in some cultivars. In this case the primary effect was through enhancement of the mean weight per grain. In general post-anthesis application of ethephon does not affect the number of grains $spike^{-1}$. Overall, post-anthesis application of ethephon may be used as a managerial tool to increase the grain yield of at least some spring barley cultivars.

Data collected from two greenhouse-experiments suggested that the peduncle perfusion system, developed in this study, will be useful for studies on nutrients and metabolism effectors in a variety of hollow-stemmed grass species.

Section 12

CONTRIBUTIONS TO KNOWLEDGE

The apical development of spring barley had been poorly characterized under North American field conditions. We have supplied new information in this area and have also addressed and quantified the effects of CCC and ethephon on the apical development and on tip abortion, which had not previously been tested. Our report on the effects of CCC and ethephon on the tillering pattern and contributing of tillers to grain yield added to the small body of current literature on this subject. The post-anthesis application of ethephon to spring barley added new insight into the use of PGR in Agriculture. Finally, we successfully developed a system for introducing various substances into hollow-stemmed cereal crops and studying their effects on the grain development.

The following are considered to be specific contributions to original knowledge:

1. The time and the duration of key stages of apical development in spring barley were illustrated for the first time under north eastern North American field conditions. The development is distinguished by a relatively short period of time for each stage and for the overall phase. Approximately 30 spikelet primordia (nodes) were initiated in 16 d with a rate of 1.9 primordia d^{-1}, a distinct contrast with previously reported data from Europe.

2. Early application of CCC slowed the apical development of the main shoot, and reduced the number of tip primordia that eventually

aborted. This is the first report of this phenomenon.

3. This work contains the first report that early application of ethephon severely suppressed apical development of the main shoots but the effects observable at the whole plant level were not detected until flag leaf emergence.

4. This research made the first clear demonstration that early application of ethephon or CCC often increased the number of spike-bearing shoots through promoting tillering, not by improving tiller survival, a situation often incorrectly reported, while application of CCC or ethephon at ZGS 39 increased spike number via enhanced tiller survival.

5. We clearly established that early or timely application of CCC or ethephon did not efficiently improve grain yield under current cultural practices and the climatic conditions under which this work carried out (under continental climatic conditions of Eastern Canada).

6. Ethephon application at ZGS 39 was effective in reducing plant height and lodging of spring barley, but did not increase grain yield even under conditions of severe lodging. This situation was only noticed recently in Western Canada.

7. Post-anthesis application of ethephon increased grain mass and yield, a phenomenon reported for the first time in this work.

8. The peduncle perfusion system was successful as a technique for studying the effects of a wide range of substances on metabolism during grain fill. It has potential application to all hollow-stemmed species.

Section 13

SUGGESTIONS FOR FUTURE RESEARCH

Much work remains to be done in the interface of PGR physiology research and cereal crop management research. Specifically, the investigations that could follow the work reported here are:

1. Lower than recommended PGR rates for control lodging, applied at specific stages of the apical development is worthwhile to investigate.

2. Investigation of the effects of PGR application on tip abortion and the subsequent impact on the number of grains per spike would be useful in understanding the mechanisms of tip abortion. This can be done by series sampling shortly before heading until 10 d after anthesis.

3. An experiment should be conducted to investigate the effects of date and rate of post-heading ethephon application to barley (possibly other cereal) cultivars to determine the economic usefulness of late ethephon application on grain production.

4. Other sources of PGR should be tested for early tillering promotion in cereal crops. For instance, paclobutrizal functions as anti-gebberillin. Brassinosteroids have been tested and used for wheat and barley production in Japan, China and other Asian countries. It would be of interest to test these promising PGR for cereal production under North American conditions.

5. The peduncle perfusion system could be used as a tool to

increase our better understanding of source-sink relations by hormonal manipulation of sink development. PGR and other metabolism effectors could be delivered into peduncle or lower internodes at various stage of grain fill or earlier development of cereal crops.

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