ASSIMILATE PARTITIONING, TILLERING, AND YIELD COMPONENTS IN BARLEY TREATED WITH ETHEPHON

BY

JACK MOES

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

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ASSIMILATE PARTITIONING, TILLERING, AND YIELD COMPONENTS IN BARLEY TREATED WITH ETHEPHON.

Supervisor: Dr. E.H. Stobbe, Department of Plant Science.

Ethephon [(2-chloroethyl)phosphonic acid] effectively reduces lodging in barley, but may also have positive or negative results on yield components and yield even if lodging does not occur. Studies were undertaken to determine the effects of ethephon on tillering, photoassimilate partitioning, spikes plant^{-1}, kernels spike^{-1}, and kernel weight for barley grown under Manitoba conditions. In 1987, 1988, and 1989, Argyle and Samson barley were grown at Winnipeg at 100 and 300 plants m^{-2} and treated with ethephon at Zadoks GS 35 and/or 45. Tiller emergence and senescence was observed throughout each growing season for 10 plants plot^{-1}, and yield components were determined at harvest. The two cultivars responded similarly to ethephon in all three years of the study. Hand harvested grain yields were either unaffected or reduced by ethephon, but combine harvested grain yield tended to be increased in 1989 when lodging was severe in untreated plots. Ethephon promoted the growth and emergence of tiller buds, resulting in increased shoots plant^{-1} each year and at each density; however, this promoted tiller growth resulted in increased spikes plant^{-1} for ethephon treated plants only in 1987 for both densities. A ^{14}C-assimilate partitioning study in 1989 indicated that ethephon's promotion of tiller bud growth may be in response to increased availability of assimilate at tiller bud sites. Ethephon did not enhance survival of tillers which would otherwise have senesced; in 1989, ethephon promoted senescence of some

early tillers with the consequence that spikes plant^{-1} was not increased despite promoted late tiller appearance. Kernels spike^{-1} was consistently reduced by ethephon, related both to ethephon's gametocidal properties as well as to the presence of late-emerged tillers with relatively fewer kernels than early emerged tillers. Kernel weight was reduced, unaffected, and increased by ethephon in 1987, 1988, and 1989, respectively. The increase in 1989 was likely due to the reduction of lodging by ethephon, while evidence from the ^{14}C-assimilate partitioning study suggested that reductions in kernel weight such as in 1987 may be due to competition between developing spikes and late tillers which appear in response to ethephon. The risk of negative responses to ethephon makes the use of ethephon in Western Canada advisable only when the risk of severe lodging is known to be high.

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1. GENERAL INTRODUCTION.

The plant growth regulator ethephon is an effective anti-lodging agent for barley when applied just prior to heading. The lodging resistance of barley treated with ethephon has been attributed to the shortening of the plant which occurs when ethephon reduces the extent to which the uppermost internodes elongate.

The application of ethephon to barley for lodging control also results in other effects on crop growth. Often ethephon application results in an increase in grain bearing shoots $plant^{-1}$ or $area^{-1}$ and a reduction in kernels $spike^{-1}$. Kernel weight is sometimes increased when lodging is prevented by ethephon application, but decreased when ethephon is applied in the absence of lodging. The net result of these individual yield components effects on grain yield may be positive, nil, or negative.

While it has been suggested that ethephon increases spikes $plant^{-1}$ by preventing tiller senescence, it has been observed that ethephon often promotes the emergence of late tillers. The significance of these late tillers with respect to the final spike population and grain yield is not known, and the conditions under which they are promoted requires further elucidation. The physiology underlying the reductions in kernel number associated with ethephon application appears to be well understood, but factors determining the degree to which this occurs are unclear. The reason for the reduction in kernel weight sometimes observed when ethephon is applied in the absence of lodging is not known.

The research reported in this document was undertaken with the following objectives: to determine whether ethephon enhances survival of early tillers, or promotes the growth and development of late tillers in order to increase spikes plant^{-1}; to determine the significance of the extra tillers with respect to yield; to elucidate the causes of reductions in kernels spike^{-1} with ethephon application; to determine whether changes in partitioning in ethephon treated plants promote availability of assimilates at tiller buds and thus promote their growth; and to investigate the causes of kernel weight reductions observed with ethephon application. Besides contributing to an understanding of the physiology of ethephon in cereal crops, this research will also contribute to our ability to make intelligent recommendations regarding the use of ethephon by barley producers under Canadian Prairie conditions.

2. LITERATURE REVIEW.

2.1 Nature and Activity of Ethephon.

Ethephon [(2-chloroethyl)phosphonic acid] is essentially stable in aqueous solutions with pH less than 4 (Cooke and Randall, 1968; Edgerton and Blanpied, 1968; Warner and Leopold, 1969). At pH greater than 4, ethephon breaks down to release ethylene, and chloride and phosphate ions (Cooke and Randall, 1968; Domir and Foy, 1978a; Maynard and Swan, 1963; Warner and Leopold, 1969; Yang, 1969); the plant growth regulator properties of ethephon have been attributed to the release of ethylene in plant cells. The release of ethylene from ethephon is not instantaneous, with a very slow release occurring even at pH less than 4 (Edgerton and Blanpied, 1968). The rate of ethylene evolution from buffered solutions, from cherry foliage (Olien and Bukovac, 1978), and from tomato foliage (Lougheed and Franklin, 1972) increases with temperature.

Kreitsberg et al. (1984) found that more than 50% of ethephon applied did not not penetrate the leaf in the first 3 days after application, and 27% could be washed off the leaf after 9 days. When ethephon was applied to grape vines, 62% of that applied could easily be washed off leaf surfaces after 7 days (Martin et al., 1972).

Working with ^{14}C-ethephon in tobacco, Domir and Foy (1978b) found that ethephon penetrated leaf tissue easily, and was translocated primarily acropetally from the point of treatment, with no ^{14}C activity anywhere but in the treated leaf. In contrast, when Kreitsberg et al. (1984) applied ethephon to the coleoptile and first leaf blade of winter rye seedlings, they were able to detect small amounts of apparently undegraded ethephon in the second and third leaves 72 to 216 hours

later, after those leaves had emerged. Others have reported translocation of ethephon to immature tissues or fruits (Edgerton and Hatch, 1972; Martin et al., 1972; Weaver et al., 1972; Yamaguchi et al., 1971).

The peak release of ethylene occurred in the first 24 hours after application when tobacco leaves were treated with ethephon (Domir and Foy, 1978a; 1978b). Ethylene evolution also peaked in the first day after treatment of winter rye seedlings (Kreitsberg et al., 1984). When soybean disks were incubated in ethephon solution, ethylene release was high for the first day, peaked on the second day, and fell to less than 5% of the peak level by the sixth day (Lurssen, 1982). Edgerton and Hatch (1972) and Weaver et al. (1972) differentiated between ^{14}C-ethylene released from ^{14}C-ethephon, and unlabelled ethylene released in response to elevated ethylene levels (autocatalysis). They reported that the peak release of labelled ethylene occurred in the first 24 hours after ethephon application, but unlabelled ethylene levels fell more gradually after several days.

Reports of ethephon metabolism to inactive and/or transportable forms vary in their conclusions depending on which species was studied. Ethephon was apparently not metabolized in tobacco (Kreitsberg et al., 1984), grapes (Weaver et al., 1972), tomato (Yamaguchi et al., 1971), apple, or cherry (Edgerton and Hatch, 1972). However, metabolites of ^{14}C-ethephon have been detected in summer squash (Yamaguchi et al., 1971), peach (Abdel-Gawad and Martin, 1973), and rubber (Archer et al., 1973). Lavee and Martin (1974) attributed the metabolism in peach tissue to chemical or physical reactions rather than to enzymatic

interactions with the living tissue. No information is available as to sites of ethephon metabolism or forms in which it may be translocated.

2.2 Observed Responses to Ethephon in Many Species.

Aside from its effects in cereal crop species, ethephon has been reported to have many effects in many species. A review of the Bibliography of Agriculture (USDA, National Agriculture Library; Silver Platter AGRICOLA CD-ROM version) over the last 10 years shows at least 450 citations mentioning more than 100 species in which ethephon was used.

DeWilde (1971) reviewed the uses of ethephon, applied at various stages of growth to various species: ethephon had been found to affect flower induction and sex expression, retard vegetative growth and decrease apical dominance, overcome seed or bulb dormancy, induce or accelerate leaf, flower, and fruit abscission, induce or accelerate fruit ripening, increase disease resistance, increase fruit bud hardiness, and increase latex flow.

2.3 Observed Responses to Ethephon in Cereal Crop Species.

2.3.1 Lodging Resistance.

Many reports attest to the effectiveness of ethephon in reducing the susceptibility of cereal plants to lodging when it is applied during the early to late boot stage. These will not be discussed in this review.

Lodging of cereal plants can be a consequence of loss of root anchorage or more often by structural failure of the straw (Neenan and Spencer-Smith, 1975). When rain, wind, or other causes apply forces perpendicular to cereal grain stems, the stems bend; if the bending

exceeds a resistance determined by Young's modulus and the outer diameter of the straw, the stem buckles. Because the force low on a cereal stem is proportional to the fourth power of the height of the stem (Pinthus, 1973), short plants are more resistant to lodging than tall plants, all other stem physical characteristics being equal. Ethephon effectively reduces stem elongation, resulting in shorter plants which are more resistant to lodging.

Ethephon and/or ethylene has been observed to reduce cell elongation in *Avena sativa* (VanAndel and Verkerke, 1978), and pea epicotyls (Burg et al., 1971). Ethylene induced by physical restriction of *Phaseolus vulgaris* growth reduced leaf and internode elongation (Hillman and Yeang, 1979). Ethephon and ethylene have both been reported to promote stem thickening (Selga et al., 1985; Abeles, 1973). Selga et al. (1985) observed increased dry matter accumulation per unit of stem length in rye treated with ethephon, although Knapp et al. (1987) reported that a similar accumulation in wheat stems was in the form of non-structural carbohydrate. This effect of ethephon may contribute to lodging resistance.

2.3.2 Yield and Yield Components.

Various grain yield responses (positive, negative, or nil) to ethephon have been reported for different cereal crops (Table 2.1). Cereal grain yield can be thought of as the product of several components, namely, the average number of spikes per unit area, the average number of kernels per spike, and the average weight of individual kernels. Ethephon application has been reported to influence each of these yield components for various cereals (Table 2.2). The most commonly reported responses are increases in spikes area^{-1}, and

Table 2.1. Examples of grain yield responses to ethephon reported for various cereal crops.

Crop	Yield Response⊖	Sources
Spring barley	+	Bahry, 1988; Dahnous et al., 1982; Entz, 1988; Simmons et al., 1988
	0	Bahry, 1988; Caldwell et al., 1988; Entz, 1988; Foy and Witt, 1987; Simmons et al., 1988; Wunsche, 1977
	-	Bahry, 1988; Caldwell et al., 1988; Simmons et al., 1988; Wunsche, 1977
Spring wheat	+	Simmons et al., 1988
	0	Dahnous et al., 1982; Simmons et al., 1988
	-	Dahnous et al., 1982; Simmons et al., 1988; Wunsche, 1977
Oat	+	
	0	Brown and Earley, 1973
	-	Brown and Earley, 1973; Wunsche, 1977
Triticale	+	Dahnous et al., 1982
	0	Dahnous et al., 1982
	-	
Winter barley	+	Hill et al., 1982
	0	Hill et al., 1982
	-	Hill et al., 1982
Winter wheat	+	Brown and Earley, 1973; Nafziger et al., 1986; Wiersma et al., 1986
	0	Brown and Earley, 1973; Cox and Otis, 1989; Knapp et al., 1987; Nafziger et al., 1986; Wunsche, 1977
	-	Brown and Earley, 1973; Knapp et al., 1987; Nafziger et al., 1986; Wunsche, 1977

⊖ Symbols "+", "0", and "-" refer to positive, null, and negative grain yield responses to ethephon, respectively.

Table 2.2. Examples of yield component responses to ethephon reported for various cereal crops.

Response⊖	Crop	Sources
Spikes Plant^{-1}		
+	barley	Bahry, 1988; Entz, 1988; Morena et al., 1988; Simmons et al., 1988; Wunsche, 1977
	wheat	Simmons et al., 1988
	oat	Wunsche, 1977
	winter barley	Hill et al., 1982
0	barley	Bahry, 1988; Entz, 1988; Simmons et al., 1988; Wunsche, 1977
	wheat	Simmons et al., 1988; Wunsche, 1977
	oat	Wunsche, 1977
	winter barley	Hill et al., 1982; Pearson et al., 1989
	winter wheat	Wunsche, 1977
-	winter wheat	Cox and Otis, 1989
Kernels Spike^{-1}		
+	wheat	Simmons et al., 1988
0	barley	Bahry, 1988; Entz, 1988; Foy and Witt, 1987 Simmons et al., 1988
	wheat	Simmons et al., 1988
	winter barley	Hill et al., 1982 Pearson et al., 1989
	winter wheat	Brown and Earley, 1973; Cox and Otis, 1989 Wunsche, 1977
-	barley	Bahry, 1988; Simmons et al., 1988; Wunsche, 1977
	wheat	Simmons et al., 1988; Wunsche, 1977
	oat	Wunsche, 1977
	winter barley	Hill et al., 1982
	winter wheat	Brown and Earley, 1973; Wunsche, 1977
Kernel Weight		
+	barley	Foy and Witt, 1987 Simmons et al., 1988
	oat	Brown and Earley, 1973
	winter wheat	Cox and Otis, 1989
0	barley	Bahry, 1988; Entz, 1988; Foy and Witt, 1987 Simmons et al., 1988
	wheat	Simmons et al., 1988
	oat	Brown and Earley, 1973
	winter barley	Hill et al., 1982 Pearson et al., 1989
	winter wheat	Brown and Earley, 1973; Cox and Otis, 1989
-	barley	Bahry, 1988; Foy and Witt, 1987; Simmons et al., 1988; Wunsche, 1977
	wheat	Simmons et al., 1988; Wunsche, 1977
	oat	Wunsche, 1977
	winter barley	Hill et al., 1982
	winter wheat	Brown and Earley, 1973; Wunsche, 1977

⊖ Symbols "+", "0", and "-" refer to positive, null, and negative yield component responses to ethephon, respectively.

decreases in kernels spike^{-1} and kernel weight. The net effect of ethephon on grain yield then depends on a balance of positive, null, or negative responses of individual yield components to ethephon.

Yield increases when ethephon application has prevented lodging have been attributed to increased kernel weight and/or increased harvestability due to the prevention of lodging (Brown and Earley, 1973; Cox and Otis, 1989; Dahnous et al., 1982; Foy and Witt, 1987; Hill et al., 1982; Simmons et al., 1988; Wiersma et al., 1986). Yield increases with ethephon application in the absence of lodging have been attributed to increased spikes area^{-1} (Bahry, 1988; Hill et al., 1982). Yield decreases with ethephon application have been attributed to reduced kernels spike^{-1} (or panicle^{-1}) and/or reduced kernel weight (Bahry, 1988; Brown and Earley, 1973; Wunsche, 1977).

Factors which have been observed to influence the type and magnitude of yield component responses to ethephon include cultivar differences (Bahry, 1988; Cox and Otis, 1989; Dahnous et al., 1982; Entz, 1988; Nafziger et al., 1986; Simmons et al., 1988; Wiersma et al., 1986), ethephon application rate (Bahry, 1988; Brown and Earley, 1973; Dahnous et al., 1982; Entz, 1988; Hill et al., 1982; Nafziger et al., 1986; Simmons et al., 1988; Wunsche, 1977), crop growth stage at time of ethephon application (Brown and Earley, 1973; Caldwell et al., 1988; Hill et al., 1982), and environment (Entz, 1988; Simmons et al., 1988; Wiersma et al., 1986).

Evidence presented in Table 2.3 suggests that moisture availability during the growing season influences the response of spikes area^{-1} to ethephon application. Increases in spikes area^{-1} which could compensate for reductions in kernel spike^{-1} and/or kernel weight tended

Table 2.3. Summary of ethephon effects on spring barley yield and yield components reported in studies from Manitoba and Minnesota.

Source	Ethephon Rate	Ethephon Timing	Ethephon Effects on:Θ Grain Yield	Spikes Plant^{-1}	Kernel Plant^{-1}	Kernel Weight	Cultivars	Growing Season Precipitation
	g ha^{-1}	ZGS						mm
Bahry, 1988					1986			
(Portage la Prairie, Manitoba)	120 -480	45	+	+	-	0	Bedford, early seeded	May- 46
			-	+	-	0	Samson, early seeded	Jun- 93
			+	+	-	0	Argyle, early seeded	Jul- 149
			0	+	0	-	Bedford, late seeded	
			-	+	-	0	Samson, late seeded	
			+	0	0	0	Argyle, late seeded	
					1987Ω			
			-	0	0	-	Bedford, early seeded	May- 39
			-	0	0	0	Samson, early seeded	Jun- 44
			-	0	-	-	Argyle, early seeded	Jul- 82
			-	0	0	-	Bedford, late seeded	
			0	0	0	0	Samson, late seeded	
			-	0	-	0	Argyle, late seeded	
Simmons et al., 1988					1984Ω			
(St. Paul, Minnesota)	420	37-45	0	+	-	-	Glenn	Apr- 76
			0	+(NS)	-	0	Morex	May- 66
			-	+	-	0	Robust	Jun- 229
								Jul- 85
					1985Ω			
	280		0	0	0	0	Glenn	Apr- 45
			0	0	0	0	Morex	May- 113
			0	0	-	+	Robust	Jun- 95
	420		0	0	-	0	Glenn	Jul- 89
			0	0	0	0	Morex	
			-	0	-	+	Robust	

Θ Symbols "+", "0", and "-" refer to positive, null, and negative yield or yield component responses to ethephon, respectively.
Ω No lodging occurred this season.

to occur under conditions of adequate moisture availability (1986 in Bahry (1988); 1984 in Simmons et al. (1988)), whereas spikes area^{-1} tended not to be increased under drier conditions, often resulting in a net negative effect on grain yield.

2.4 Tillering in Cereals.

2.4.1 Tiller Demography.

2.4.1.1 Cereal Growth Stages and Tiller Characterization.

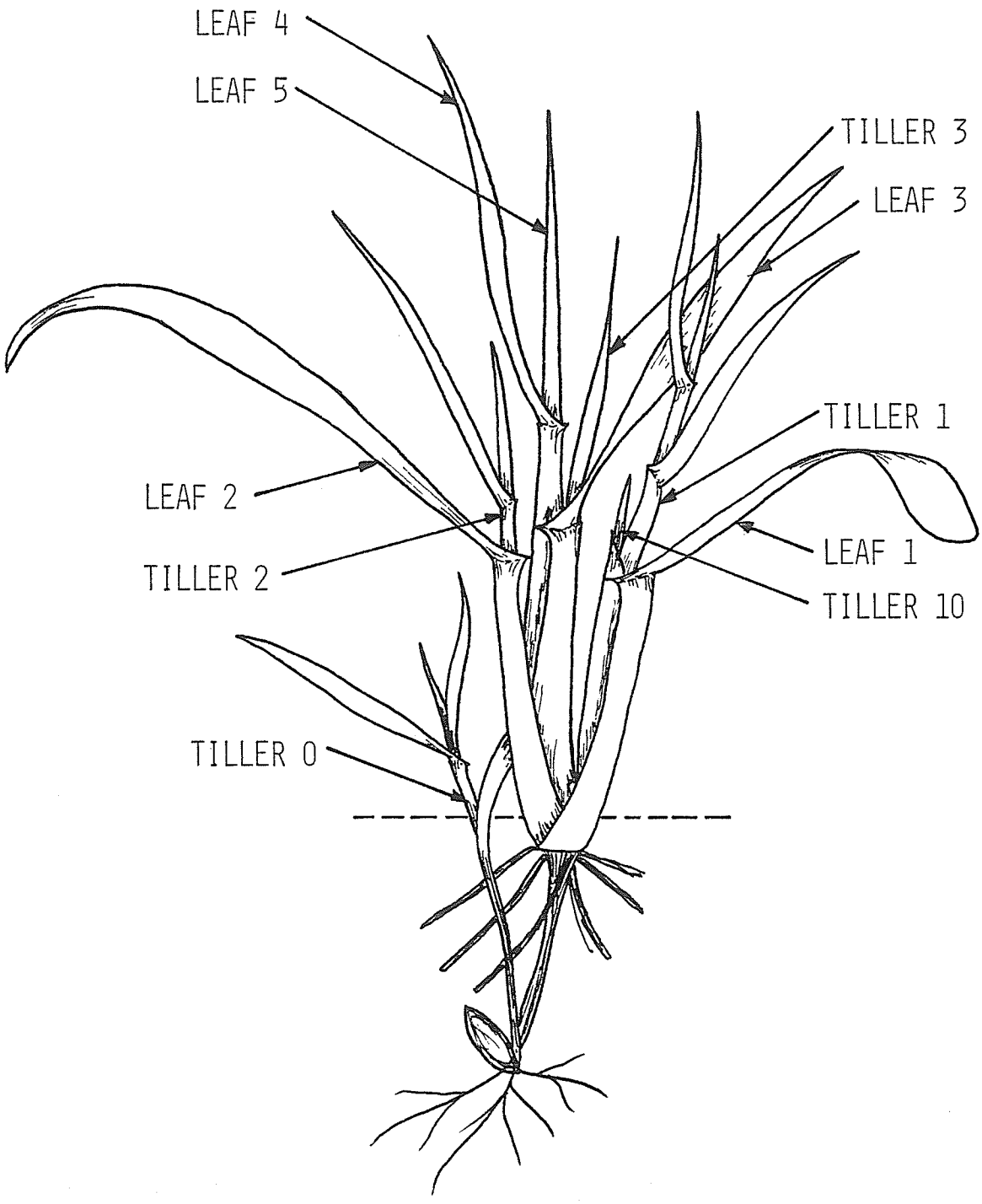
The Zadoks-Chang-Konzak decimal code for the growth stages of cereals (Zadoks et al., 1974), has become a widely used scale for the description of cereal plant growth and development. Cereal growth and development is divided into ten stages (Table 2.4), starting from dry seed to ripe, non-dormant seed. Each major stage is further subdivided to allow for a detailed description of growth.

Grass tillers arise from axillary buds, in the same way as dicot branches arise from axillary buds. The orderly and predictable pattern of appearance of cereal plant tillers is the basis of a system of tiller characterization developed by Klepper et al. (1982)(Fig. 2.1). Leaves are numbered up from the base of the main stem, 1, 2, 3, etc., and the coleoptile is designated as leaf 0. First-order tillers (ie. those arising from the main stem) are given the number of the leaf from whose axil they have developed. Leaves on tillers are numbered with a two digit number, the first digit the same as that of the tiller on which the leaf is found, and the second digit the actual leaf number on the tiller numbered up from the base of the tiller; thus leaves on tiller 1 are 10 (the prophyll), 11, 12, etc. Second-order tillers (ie those arising from a tiller) are given the two digit number of the tiller leaf from whose axil they have developed. This characterization is easily

Table 2.4. Major cereal growth stages of Zadoks-Chang-Konzak decimal code for the description of cereal growth (Zadoks et al., 1974).

Code	Stage	Stage Description
00-09	Germination	Dry seed, inbibition, germination, to first leaf just visible at coleoptile tip.
10-19	Seedling growth	Emergence of main stem leaves.
20-29	Tillering	Emergence of tillers.
30-39	Stem elongation (Jointing)	Start of elongation, stem nodes become detectable, to flag leaf blade fully emerged.
40-49	Booting	Flag leaf sheath extending, inflorescence swelling within flag leaf sheath, to awns just visible.
50-59	Inflorescence emergence	First spikelet visible to inflorescence fully emerged.
60-69	Anthesis	Anthesis progresses throughout inflorescence.
70-79	Milk development	Early grain filling.
80-89	Dough development	Late grain filling.
90-99	Ripening	Mature grain loses moisture, straw becomes brittle, seed may become dormant, then lose dormancy.

Fig. 2.1. Barley plant demonstrating tiller characterization system of Klepper et al. (1982).


LEAF 4
LEAF 5
TILLER 3
LEAF 3
TILLER 1
LEAF 2
LEAF 1
TILLER 2
TILLER 10
TILLER 0

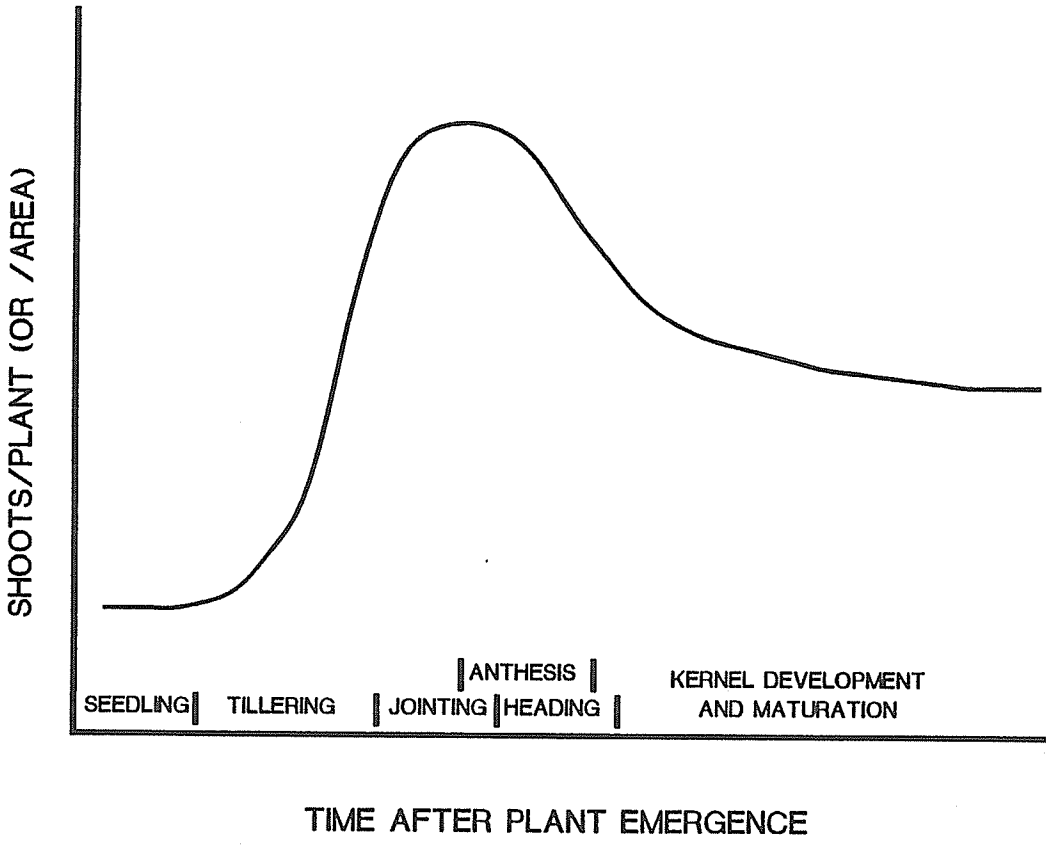
extended to third-order tillers which also sometimes appear, by using a three digit number.

2.4.1.2 Typical Seasonal Tillering Patterns.

Fig. 2.2 illustrates a typical pattern of tiller emergence, senescence, and survival. Shoots plant^{-1}, or area^{-1} rises to a maximum (influenced by the factors described below) during the tillering phase. The maximum number of shoots occurs at about the time the main stem begins to elongate, with stem elongation itself being instrumental in the suppression of emergence of further new tillers (Aspinall, 1961; Jewiss, 1972). Some of the tillers senesce, resulting in some final number of shoots which bear some amount of grain. Tiller bud elongation and emergence sometimes resumes after heading (Aspinall, 1961 and 1963; Jewiss, 1972; Kirby, 1967; Laude et al., 1967; 1968; Thorne, 1962), which appears to be enhanced by wet weather (Kirby, 1967), and by nitrogen availability (Aspinall, 1963; Thorne, 1962). Aspinall (1961) observed that tillers which appeared after heading had greatly reduced first leaf blades compared with early formed tillers, frequently elongated from nodes above the soil, and rapidly produced spikes although with fewer kernels than spikes on early tillers.

Ethephon is normally applied to barley (or other cereal plants) during the early to late boot stage, and therefore, could exert its influence on final shoot number (per plant or per unit area) at two points in the typical pattern of tiller demography: during the phase of tiller senescence, by enhancing survival of tillers which would otherwise senesce; or after spike emergence, by enhancing the growth and survival of the late tillers that appear after that time. It has been suggested that ethephon enhances survival of early tillers (Bahry, 1988;

Fig. 2.2. Typical pattern of shoots plant^{-1} (or area^{-1}) for spring type cereal plants or populations through a growing season, with major developmental events indicated (after Gallagher et al., 1976; Simmons et al., 1982; Thorne, 1962; Bremner, 1969; Cannell, 1969a).


SHOOTS/PLANT (OR /AREA)
ANTHESIS
SEEDLING
TILLERING
JOINTING
HEADING
KERNEL DEVELOPMENT
AND MATURATION
TIME AFTER PLANT EMERGENCE

Karpenstein and Scheffer, 1984; Morena et al., 1988; Simmons et al., 1988), although ethephon also promotes the appearance of late tillers (Hill et al., 1982, Netherlands, 1989).

A general pattern of potential tiller appearance after main stem emergence is that given by Klepper et al. (1982) for a winter wheat cultivar: 0, 1, 2, 00, 10, 01, 3, 20, 11, 000, 02, 100, 21, 4, 001, 010, 30, 12, 200, 101, 110, 0000, 22, 31, 5. Many of the second and third order tillers appeared simultaneously. The sequence given is generalized from growth chamber and field studies; a well tillered plant in the field is likely to exhibit only the first several tillers given in the sequence, depending on growing conditions as outlined below. The sequence given by Ishag and Taha (1974) for spring wheat is similar, although the coleoptile tiller (T0) apparently did not appear (therefore, its second and third order tillers also did not appear): 1, 2, 3, 10, 4, 20, 11, 5, 30, 21, 6, 12, 40, 31, 22. Tiller production, survival, and yield decline from first formed to last (Cannell, 1969a; Ishag and Taha, 1974; Labanauskas and Dungan, 1956). Kernels spike^{-1} and kernel weight also tend to decline from early to later formed tillers (Power and Alessi, 1978). Tillers develop more rapidly than the main stem and successive tillers moreso, resulting in a relatively synchronous maturity of tillers and main stem (Macdowall, 1973).

All other factors being equal, cultivars of oats, wheat, and barley differ in production and survival of tillers (Benbelkacem et al., 1974; Cannell, 1969a; Dewey and Albrechtsen, 1985; Kaukis and Reitz, 1955; Kirby and Faris, 1972; Simmons et al., 1982). Semi-dwarf cereal cultivars tend to produce more tillers than conventional height cultivars (Blackman et al., 1978; Lupton et al., 1974; Paquet, 1968;

Spiertz and VandeHaar, 1978). Generally, high tillering genotypes have higher shoot mortality than low tillering genotypes (Simmons et al., 1982). Some cultivars produce more tillers, but fewer survive to maturity compared with other cultivars (Kirby and Faris, 1972). Tillering capacity is a heritable trait (Benbelkacem et al., 1974; Donald, 1979; Hadjichristodoulou, 1985).

Increased levels of nitrogen fertilizer enhance tiller production and/or survival (Cannell, 1969a; Fraser et al., 1982; Garcia del Moral et al., 1984; Ishag and Taha, 1974). Ishag and Taha (1974) found that the addition of nitrogen increased production of T1 and T2 and tillering efficiency (ratio of fertile to total tillers produced). Fraser et al. (1982) observed that T3 was most affected by nitrogen in terms of enhanced production and survival, while Power and Alessi (1978) reported that nitrogen reduced mortality of T2 and T3 in the latter part of season when water was limited. Garcia del Moral et al. (1984) found that increased nitrogen at seeding enhanced production and survival of tillers, but nitrogen topdressed midway through stem elongation did not affect the number of shoots.

Increased temperatures over the range from 10 to 25^{o}C reduced tillering (Friend, 1965); the coleoptile tiller was most affected, being present on fewer plants grown at 25 or 26 than at 10^{o}C (daytime) (Cannell, 1969b; Frank and Bauer, 1982). However, Campbell and Read (1968) observed no differences in tillering of wheat grown under 27/21, 21/13, and 21/15^{o}C day/night temperature regimes.

Tillering of cereal plants is reduced by increases in plant density (Cannell, 1969a; Casal et al., 1986; Darwinkel, 1978; Fraser et al., 1982; Kaukis and Reitz, 1955; Kirby and Faris, 1972; Simmons et

al., 1982). Darwinkel (1978) found that for winter wheat, tillering per plant was favoured by low density because tillering continued over a longer period and a greater proportion of tillers produced ears.

Reduced light intensity, as by shading, reduces tiller production and survival (Campbell and Read, 1968; Fischer, 1975; Jewiss, 1972; Ong and Marshall, 1979; Rickman et al., 1985; Spiertz and Ellen, 1972). While specific tillers may be influenced to differing degrees (Cannell, 1969b), the overall sequence of tiller development is not affected (Rickman et al., 1985).

Plants grown under a low level of moisture stress exhibited more and taller tillers with thicker culms than plants grown under a high level of moisture stress (Campbell and Read, 1968).

2.4.2 Tiller Initiation and Growth.

Tillers develop from buds located in the angle formed by a leaf sheath and a stem. Elongation of the prophyll, a coleoptile-like modified leaf sheath, between the stem and the leaf sheath causes emergence of the tiller at the leaf collar, the point at which a tiller is normally first visible. Williams and Langer (1975) performed some anatomical studies of wheat tiller development and found that when they plotted length vs. time for tiller growth, for tillers which emerged the plot traced a discontinuous pattern, suggesting a critical event in tiller growth. They concluded that the critical event was the escape of the tiller bud from the cavity between the stem and leaf sheath in which the bud was located early in its development. Tillers which did not exhibit this discontinuous pattern of growth were unlikely to emerge and become an independent unit. Tiller buds which did not emerge continued to grow slowly at least until anthesis occurred on the main stem. For

example, they found that the T2 bud (T1 by Klepper et al. (1982) system) on plants treated with high light and nitrogen exhibited a greater outward thrust due to radial expansion, apparently needed to force a sufficient gap between leaf sheath and stem to allow relatively unrestricted tiller growth; the T2 bud for plants treated with low light and nitrogen reached the same stage several days later. They concluded that for the bud to escape and become an independent unit would depend on the nutritional factors and plant growth substances which govern timing of events, and suggested that those elements that are essential for cell division promote radial growth of the bud and hence promote its escape before hardening of the adjacent leaf sheath tissues.

Many studies have shown that plant growth substances influence early bud growth, and the weight of evidence suggests that the relative balance of auxin and cytokinin at tiller bud sites is important. Shifting the balance of auxin and cytokinin in favour of cytokinin promoted tiller bud outgrowth on oat stem segments, with the balance shifted by either inhibiting auxin transport or adding cytokinin (Harrison and Kaufman, 1980; 1984). For intact oat plants, gravistimulation, decapitation, and inflorescence emergence, all of which are thought to reduce auxin concentration at tiller buds, promoted tiller bud outgrowth (Harrison and Kaufman, 1980). Also in oats, while changes in free or bound IAA were not correlated with tiller bud release, levels of zeatin-riboside were positively correlated with tiller bud release (Harrison and Kaufman, 1983). Zeatin-riboside (an active cytokinin) increased with decrease in zeatin-riboside-glucoside (an inactive cytokinin metabolite) shifting the auxin-cytokinin balance

in favour of cytokinin. Auxin transport inhibitor or benzyl adenine (a cytokinin) caused tiller bud outgrowth in a sorghum variety normally exhibiting strong apical dominance, whereas auxin inhibited tiller bud outgrowth in a variety with weak apical dominace, also providing evidence for an auxin-cytokinin balance theory for regulation of tiller bud growth (Isbell and Morgan, 1982).

Other plant growth substances may act as "modulators" of tiller bud outgrowth promoted by a favourable balance of auxin and cytokinin, with abscisic acid inhibiting cytokinin induced outgrowth (Harrison and Kaufman, 1980; 1984), and gibberellic acid promoting cytokinin induced outgrowth (Harrison and Kaufman, 1980; Isbell and Morgan, 1982).

Ethylene also operates in the outgrowth of tiller buds. Ethephon application directly on axillary buds of decapitated *Phaseolus vulgaris* plants inhibited bud outgrowth, and ethylene levels decreased in the stem after decapitation (Yeang and Hillman, 1982). A decline in ethylene evolution was correlated with bud outgrowth in peas (Blake et al., 1983). In oat stem segments, ethylene inhibited bud outgrowth, apparently by inhibiting cytokinin transport to the bud and by promoting cytokinin catabolism at the bud (Harrison and Kaufman, 1984). In contrast, ethylene inhibited transport of auxin to the bud, thus promoting bud outgrowth. Others have also shown ethylene to be an auxin transport inhibitor (Burg et al., 1971; Beyer and Morgan, 1971).

Mechanical perturbation of *Pharbitis nil* internodes stimulated ethylene production in the internodes within 2 hrs, with restricted main shoot growth following within 24 hrs, and with lateral bud outgrowth following within 48 hrs, suggesting a cause and effect relationship between the stem growth restriction and the lateral bud release (Prasad

and Cline, 1985). Physical restriction of *Phaseolus vulgaris* internode elongation caused elevated ethylene levels in shoots and promoted bud outgrowth (Hillman and Yeang, 1979). Possibly, reduced auxin transport to axillary buds contributed to outgrowth in these last two examples. Taken together, these results suggest that elevated ethylene levels at axillary buds are inhibitory to bud outgrowth, while elevated ethylene levels acropetal to axillary buds may promote bud outgrowth.

The importance of stem elongation in tiller bud outgrowth in wheat was demonstrated by Jewiss (1972), who found increased tillering when wheat plants were treated with chlormequat chloride (CCC), which inhibited stem elongation, and decreased tillering when plants were treated with gibberellic acid (GA_3), which promoted stem elongation. Observations of this type led Johnston and Jeffcoat (1977) to argue for an understanding of tiller bud outgrowth based on nutrient and assimilate availability, although they themselves observed outgrowth to be inhibited by auxin and enhanced by cytokinin. They suggested that rapid shoot development diverted assimilate from buds, thus explaining inhibition of bud growth with the onset of stem elongation as observed by Aspinall (1961) and Jewiss (1972). Patrick (1972) showed that elongating internodes formed major sinks for the leaves attached at either node. Decreased export of ^{14}C-assimilate from main stem to tillers at the onset of stem elongation has been observed for barley (Lauer and Simmons, 1985).

With the further observation that after the inflorescence emerged, the flag leaf became its primary assimilate supplier (Patrick, 1972; Wardlaw, 1965), Johnston and Jeffcoat (1977) suggested that competition for photosynthate between tiller buds and the inflorescence and

elongating stem was reduced when the inflorescence emerged, allowing tiller bud outgrowth. The effect of CCC and GA_3 in promoting and inhibiting bud outgrowth, respectively (Jewiss, 1972), could then be due to enhanced or reduced assimilate availability with inhibited and promoted stem elongation by CCC and GA_3, respectively. Johnston and Jeffcoat's (1972) suggestions find support in the work of Aspinall (1963) who found that the removal of developing kernels from the infloresence promoted tillering, while the application of auxin did not affect tillering. Laude (1975) attributed the suppression of tiller buds by young leaves to auxin produced by the young leaves, but the suppression could also be related to the assimilate requirements of the young leaves.

Jewiss (1972) argued against a theory of tiller bud growth regulation based only on changes in assimilate movement, having observed that the auxin inhibitor tri-iodobenzoic acid (TIBA) promoted bud outgrowth within a few hours, while changes in bud weight or ^{14}C-assimilate movement into buds did not appear until later. Woodward and Marshall (1988) pointed out that TIBA application had no obvious effect on stem elongation; however, Jewiss (1972) observed changes in ^{14}C-assimilate movement with TIBA application. Woodward and Marshall (1988) also argued against a nutritive theory explaining tiller bud growth, although they recognized that competition for assimilates would affect the rate of bud growth. They attributed the bud outgrowth promoted by ethephon to an inhibition of auxin transport by ethylene, thereby increasing the cytokinin to auxin ratio at tiller bud sites, which they claimed appeared independent of any growth retarding effect on the main shoot.

Plant growth substance balances and assimilate availability evidently both contribute to tiller bud suppression or outgrowth, although the exact mechanisms are unclear. It is clear that tillers depend on the main stem for assimilates for sustained growth, thus competing with young leaves and the inflorescence on the main stem for limited assimilate resources. A high percentage of ^{14}C-assimilate from the lower leaves of the main stem was incorporated in tiller ears of wheat (Rawson and Hofstra, 1969). Removal of barley tillers resulted in main stems with more and heavier kernels (Chafai El Alaoui et al., 1988; Kirby and Jones, 1977). Tiller removal in wheat also led to main stem yield increases, primarily due to an increased number of kernels per spikelet (Kemp and Whingwiri, 1980; Mohamed and Marshall, 1979). Removal of green leaves from barley main stems decreased tiller dry weight (Aspinall, 1963). Removal of younger leaves from wheat main stems promoted tiller bud outgrowth, delayed tiller senescence, increased the number of tillers surviving the heading stage, and resulted in resumption of tillering after heading (Laude, 1975). Mature tillers may (Lupton, 1966) or may not (Rawson and Hofstra, 1969) become autotrophic.

2.4.3 Tiller Survival or Senescence.

As discussed earlier, not all cereal tillers which emerge survive to produce grain. Garcia del Moral et al. (1984) observed in winter barley that tillers which were less than one third of the height of the main stem at the end of stem elongation failed to produce ears, with a close correlation over years, nitrogen treatments, and cultivars, implying an empirical critical survival height.

Tiller senescence without the production of an inflorescence has been attributed to shading of young tillers (Spiertz and Ellen, 1972), and to shifts in partitioning of photoassimilates (Lauer and Simmons, 1985; Simmons and Lauer, 1986). The latter research indicated a ^{14}C-assimilate translocation shift from tillers to elongating internodes of the main stem, which seemed to contribute to tiller senescence. Ong and Marshall (1979) proposed shading of young tillers combined with the shift in photoassimilate translocation away from tillers to the elongating main stem as contributing to tiller senescence.

Recently, Lauer and Simmons (1989) reported a reduction in the rate of leaf appearance on non-surviving tillers 3-4 weeks after crop emergence but before any appreciable shading of tillers took place, and concluded that lack of light did not trigger tiller senescence. They suggested that changes in light quality triggered tiller senescence, citing the work of others which showed that increases in the ratio of red to far-red light favoured tiller production and survival (Casal, 1988; Casal et al., 1986; Deregibus et al., 1985), while increases in far-red light reduced production and enhanced senescence of tillers (Kasperbauer and Karlen, 1986). The ratio of red to far-red light varies naturally with time of day and canopy density (Casal et al., 1986; Deregibus et al., 1985; Kasperbauer and Karlen, 1986).

The competition between tillers and main stem kernel development for assimilates (Aspinall, 1963; Chafai El Alaoui et al., 1988; Kemp and Whingwiri, 1980; Kirby and Jones, 1977; Laude, 1975; Mohamed and Marshall, 1979; Rawson and Hofstra, 1969) has led to the conclusion that tillers which senesce without contributing to grain yield should be considered wasteful of resources (Kirby and Jones, 1977). However,

Lauer and Simmons (1988) treated barley tillers with $^{14}CO_2$ and found that non-surviving tillers translocated more assimilate to the main shoot than surviving tillers. Until 33-38 days after emergence the main stem also received substantial portions of tiller photoassimilate, mostly received by emerging main stem leaves, indicating that non-surviving tillers are not completely unproductive.

2.5 Gametocidal Properties of Ethephon in Cereals.

Ethephon has been investigated for its potential as a chemical male sterilant in hybrid wheat (Fairey and Stoskopf, 1975; Hughes, 1975; Hughes et al., 1978; Jan and Rowell, 1981; Rowell and Miller, 1971; 1974), barley (Law and Stoskopf, 1973; Stoskopf and Law, 1972), and triticale (Nelson, 1975; Sapra et al., 1974) breeding programs. In wheat, 500 ppm applied in pre-boot or boot stage resulted in significantly reduced seed set, and 1000-3000 ppm resulted in virtually no seed set (Note - 1000 ppm is equivalent to about 900 g ha^{-1}, about four times the rate recommended in Manitoba for lodging control) (Rowell and Miller, 1971). In the same study, cultivars differed in susceptibility, with one requiring as little as 100 and 250 ppm in pre-boot and boot stages, respectively, to significantly reduce seed set.

One of the difficulties encountered in the use of ethephon as a male sterilant was its relatively precise timing requirements to achieve full male sterility. The use of a granular form of ethephon required less precision in time of application, presumably because uptake and release would be expected to occur over a longer period of time than with a foliar applied solution (Fairey and Stoskopf, 1975). Another problem also arose in that, at the relatively high rates of ethephon required, head emergence was often incomplete (Hughes et al., 1974; Law

and Stoskopf, 1973). Therefore, Hughes et al. (1974) recommended that to induce full male sterility in wheat with full emergence of sterilized ears, 1000-2000 ppm ethephon must be applied before meiosis begins in pollen mother cells in basal florets of the oldest spikelets.

Stoskopf and Law (1972) observed three types of gametocidic responses in wheat treated with ethephon: all 3 anthers per floret sterile with no pollen released, 1 or 2 anthers sterile and remaining anther retarded about 7 days in pollen release, and all 3 anthers retarded about 7 days in pollen release.

Bennett and Hughes (1972) described the effect of ethephon on pollen development. In normal development in wheat anthers after meiosis, pollen grain mitosis (PGM) 1 results in a diffuse vegetative nucleus (no further division), a generative nucleus which comes to lie opposite the germination pore, and a vegetative nucleus. In PGM 2, the generative nucleus divides to produce two sperm nuclei. Starch granules appear after PGM 1 and increase in size and number until they pack the pollen grain by PGM 2; the starch granules persist until dehiscence. At dehiscence, the pollen grain is tri-nucleate. Anthers at or after meiosis when treated with ethephon completed normal pollen development, and anthers dehisced normally and at the expected time. If treated 1-5 days before meiosis, meiosis and PGM 1 proceeded normally, but abnormal development was apparent just before PGM 2: starch granules began to degrade, and in PGM 2, both nuclei divided, but none formed sperm nuclei; further divisions resulted in as many as 8 nuclei.

Treatment of barley with ethephon at the pollen mother cell stage frequently led to degeneration of the sporogenous tissues, sometimes also causing additional mitotic divisions and the formation of abnormal

cell walls; treatment after meiosis often caused degeneration and collapse of the microspores (Colhoun and Steer, 1983). These authors concluded that ethephon acted through a general disruption of activities within the anther locule, rather than by specific actions on one or two processes, and that gametocidic activity seemed to depend on upsetting the growth regulator balance within the anther.

In barley spikes, florets in the mid-section are more advanced than in the basal section, and the apical section is least advanced with respect to state of differentiation at a given time (Bonnett, 1935). With ethephon normally being applied sometime during the boot stage, it would seem likely that some florets in the basal and apical regions of the developing inflorescence would be at the sensitive pre-meiotic pollen mother cell stage, and hence prone to male sterility due to the ethephon application. This is then very likely to result in reduced kernel set, especially in a self-fertilized species such as barley, although in cross-fertilized species such as wheat, the effect may be obscured (Brown and Earley, 1973).

2.6 Summary.

When lodging is prevented by ethephon, kernel weights and harvestable yield may increase, and the ease of harvesting may also be enhanced. The application of ethephon to cereals confers lodging resistance, but may also result in positive or negative effects on spikes plant^{-1} (or area^{-1}), kernels spike^{-1}, and kernel weight, with net negative, null, or positive effects on grain yield (section 2.3.2).

It has been suggested that increases in spikes plant^{-1} with ethephon application are due to prevented senescence of early appearing tillers (section 2.4.1.2). However, given the recent observation of

Lauer and Simmons (1989) that signs of senescence on non-surviving tillers were apparent as early as 3-4 weeks after crop emergence, it is unlikely that ethephon application at the boot stage, when senescence is already visually apparent, could prevent tiller senescence. Indeed, at least one report shows that tiller senescence was promoted by ethephon (Cox and Otis, 1989). It is most likely that ethephon induced increases in spikes plant^{-1} are due to promoted appearance of tillers after heading. The relative contribution of such late-appearing tillers to yield is unknown.

Ethephon exerts its influence on plant growth by releasing ethylene in plant cells. Ethylene is known to inhibit basipetal transport of auxin, possibly altering the balance of cytokinin and auxin at tiller bud sites; this has been suggested as a reason for the promoted growth and emergence of tiller buds in cereal plants treated with ethephon (section 2.4.2). Changes in assimilate partitioning with stem elongation have also been implicated in the promoted growth of tiller buds, which results from enhanced assimilate availability to tiller buds. The precise mechanisms by which ethephon promotes tiller bud growth are not clear, but may involve changes in both plant growth substance balances and assimilate partitioning.

Gametocidal properties of ethephon are well known, and likely contribute to the reductions in kernels spike^{-1} often observed in cereal crops treated with ethephon. Factors determining the degree to which these properties affect kernels spike^{-1} and yield in barley treated with ethephon are not known.

The reasons for reductions in kernel weight associated with ethephon application are unknown. Given that ethephon's direct effect

on plant metabolism by elevating ethylene levels is relatively short lived (section 2.1), application of ethephon to cereals at the boot stage is unlikely to exert a direct influence on kernel filling. However, the effects of ethephon on promotion of late tiller emergence (section 2.3.2) may contribute to explaining reductions in kernel weight. First, late formed tillers tend to have reduced kernel weight compared with the main stem and early formed tillers (Cannell, 1969a), probably due to the faster rate of development of the former (Macdowall, 1973). Second, the observation that removal of barley tillers resulted in a main stem with more and heavier kernels (Kirby and Jones, 1977; Chafai El Alaoui et al., 1988), suggests that the competition between tillers and main stem kernel development for assimilates may also contribute to the observed reductions in kernel weight with ethephon application where tillering has been promoted.

3. MATERIALS AND METHODS.

3.1 Cultural Practices.

Barley was seeded at the field research site at the University of Manitoba's Fort Garry Campus (Winnipeg, MB) on May 9, 1987, May 13, 1988, and May 12, 1989. The soil type was Riverdale clay (mollic cryofluvent), and the fields used each year were in black summer fallow in the previous season.

A 2 m Noble hoe-type seed drill (Noble Equipment Co., Nobleford, Alberta) with a row spacing of 0.2 m was used, adapted for plot work with a cone spreader. The plot area was 2 m wide by 9 m in length, later cut back to 7-7.5 m to provide pathways between blocks. A space of 0.5 m was left between plots to allow for working area.

Fertilizer was applied with the seed to supplement soil levels according to soil test results taken in the last week of April in each year (Table 3.1). On May 22, 1987, MCPA herbicide (2-methyl-4-chlorophenoxyacetic acid) at 625 g ha^{-1} was applied as an overall spray to control broadleaf weeds. Additional weed control in 1987, and all weed control in 1988 and 1989, was performed by hand-hoeing as necessary.

3.2 Yield and Yield Component Studies.

3.2.1 Experimental Design.

The experiment was set up as a factorial in randomized complete blocks with four replications. The first factor was cultivar, with Argyle and Samson chosen on the basis of their apparent different responses to ethephon in prior studies (Bahry, 1988), where the yield of Argyle tended to increase and the yield of Samson tended to decrease with ethephon application. The second factor was plant density, with

Table 3.1. Soil fertility as indicated by soil test results and as banded with the seed at the time of seeding.

Year	Test/Added	Nutrient			
		N	P	K	S
		kg ha^{-1}			
1987	Test Result⊖	91	31	819	56
	Banded	24	37	15	--
1988	Test Result	84	49	855	33
	Banded	18	39	15	9
1989	Test Result	179	49	828	72
	Banded	18	18	7	5

⊖ Test results given in terms of NO_3-N and SO_4-S in top 60 cm, P (bicarbonate test) and K (ammonium acetate exchangeable) in top 15 cm.

plots being overseeded then thinned to either 300 or 100 plants m^{-2}; thinning to the desired densities was performed on a two row by 2.5 m (1 m^2) "observation area" and the two adjacent rows. The third factor was ethephon [(2-chloroethyl)phosphonic acid](Rhone-Poulenc, Research Triangle Park, North Carolina) treatment, in which ethephon was either not applied, applied at Zadoks growth stage 35 (mid-stem elongation)(except in 1989), or applied at Zadoks growth stage 45 (mid-boot stage). The ethephon was applied at a rate of 240 g ha^{-1} in approximately 100 l H_2O ha^{-1} using a portable CO_2 pressurized sprayer (4-nozzle boom covering 2 m).

3.2.2 Observations Made.

3.2.2.1 Tiller Emergence and Senescence.

After the barley emerged, ten plants were randomly selected within the 1 m^2 observation area of each plot, for observation of tillering patterns through the growing season. At intervals of two to eleven days, depending on how rapidly tillers were emerging, tillers emerged from their subtending leaf sheaths were labelled with colour-coded wire loops, and the date of emergence was recorded. In cases where a tiller was emerged but not yet large enough on which to place a wire loop, the date was recorded and the wire loop was placed on the tiller at a later date. The colour-coding of wire loops conformed to the tiller characterization system of Klepper et al. (1982). When a tiller senesced, the date when senescence was first observed was recorded; senescence of the youngest leaf on a tiller was taken as a sign of tiller senescence.

Individual tillers (ie. 1, 10, 2, 3, etc.) and the total number of live shoots (main stem and tillers) per ten plant sample were counted for each observation day.

3.2.2.2 Lodging and Head Counts.

When lodging occurred, the degree of lodging was periodically characterized for each plot using the Belgian Lodging Index:

$$\text{Lodging Index} = S \times I \times 0.2$$

S = area lodged (1 = none, to 9 = total)

I = lodging intensity (1 = upright, to 5 = flat)

(Oplinger et al., 1985, as cited by Wiersma et al., 1986). A count of the number of heads per m^2 was taken prior to harvest, using the 1 m^2 observation area chosen for tiller emergence observation and yield component assessment.

3.2.2.3 Tiller Bud Development.

In 1988 and 1989, ten plants were sampled for each cultivar and plant density combination at Zadoks GS 45. These plants were dissected and the locations (according to the tiller characterization system being used) of each emerged tiller and each non-emerged tiller bud were recorded.

3.2.2.4 Floret Sterility.

In 1988 and 1989, 8-10 main stem heads were sampled from ethephon treated and untreated plots for each cultivar at 300 plants m^2, at approximately three weeks after ethephon application. The number of developing kernels at each rachis node was recorded, as well as the number of florets which aborted prior to fertilization.

3.2.2.5 Yield Component Assessment.

When plants matured, each grain bearing shoot from each of the ten plants under observation for tiller emergence was individually harvested. Each spike was individually threshed using a single head thresher/cleaner. An additional sample of forty consecutive plants was harvested from the 1 m^2 observation area in 1987 and 1988, and each spike from these samples was also individually threshed.

Yield component assessment consisted of documenting kernels $spike^{-1}$, total grain dry weight for each grain bearing spike, and spikes $plant^{-1}$. Grain dry weights were recorded after the grain was dried at 130°C for 21 hours (ASAE, 1987). Average single kernel weight for each spike was calculated from kernels $spike^{-1}$ and total grain dry weight.

The remainder of the barley grain in the 1 m^2 observation area was harvested, threshed, dried, and weighed. The weight obtained was added to the total grain weight in the ten and forty plant samples to give a bulk yield per 1 m^2 observation area. In 1988 and 1989, the centre six rows of each plot was harvested using a small plot combine, to provide a combine harvested yield estimate after correction for moisture content (determined for a subsample dried as above).

3.2.2.6 Weather Data.

Growing season rainfall data were collected within 0.5 km of the experiment site each year. Daily maximum and minimum temperatures were also recorded within 0.5 km of the site in 1988 and 1989; in 1987, temperature data were obtained from Environment Canada at Winnipeg International Airport, approximately 10 km distant.

3.2.3 Statistical Techniques.

Analysis of variance was performed using SAS procedures (SAS Institute, 1982) or a spreadsheet template which had been checked against a similar SAS analysis for accuracy. Orthogonal comparisons were performed where appropriate. Differences with $P<0.05$ were considered meaningful, and least significant differences ($P=0.05$) were used as the basis of comparision between treatments.

Simple correlation analyses were performed to determine the strength of relationships between yield components, bulk yield, and lodging indices.

3.3 .$^{14}CO_2$ Partitioning Studies.

3.3.1 Experimental Design.

Argyle barley was sown in plots as above on May 12, 1989, at a rate giving a plant stand of 300 plants m^2. This high density was used to obtain plants which were relatively simple morphologically, consisting of only a main stem, one or two dead tillers, and one or two non-emerged tiller buds at the time of ethephon application. Half of the plots, randomly selected, received ethephon at Zadoks GS 45 at a rate eqivalent to 240 g ha^{-1}. At 3, 10, and 21 days after ethephon application, 6-8 plants were selected from an ethephon treated plot and from an untreated plot for labelling with $^{14}CO_2$. Selection was made on the basis of uniformity with respect to the degree of stem elongation, number of leaves, and number of senesced tillers; on days 10 and 21 after ethephon application, selection criteria also included the absence of late-emerged tillers on untreated plants, and the presence of similarly developed late-emerged tillers on ethephon treated plants.

3.3.2 .$^{14}CO_2$ Labelling Procedures.

$^{14}CO_2$ was generated by the addition of excess lactic acid to $Ba^{14}CO_3$ (DuPont Canada, Mississauge, Ontario) in a manometer. The manometer consisted of two flasks joined by a tube through rubber stoppers in each flask. Each flask contained acid solution (to minimize dissolution of CO_2), and the solution was continuous through the tube joining the flasks. A small vial containing the $Ba^{14}CO_3$ was hung in the mouth of one flask and sealed in by the rubber stopper containing the tube and a septum for injecting acid. Acid was injected into the vial containing $Ba^{14}CO_3$ using a syringe inserted through the septum. As $^{14}CO_2$ was evolved, the expansion of gas forced acid solution through the tube into the second flask, hence the $^{14}CO_2$ was contained in the first flask. The amount of gas contained in the flask, consisting of some air present before evolution of $^{14}CO_2$ and the evolved $^{14}CO_2$, was such that 1 ml withdrawn through the septum with a syringe contained approximately 370 to 550 kBq of activity. On a given day, just enough $^{14}CO_2$ was evolved for use on that day.

The flag and penultimate leaf blades of a plant to be treated with $^{14}CO_2$ were enclosed in small polyethylene bags with a septum at one end and sealed to the base of the leaf blade at the other end using a small amount of Terostat putty (Teroson, Heidleberg, West Germany). Using a syringe inserted through the septum, 0.5 ml of the gas containing $^{14}CO_2$ was injected into each bag. The syringe was plunged several times to ensure mixing of $^{14}CO_2$ throughout the bag. Each bag was left in place for 30 min, during which it was manually lightly shaken several times to ensure mixing of the gas in the bag. Gas remaining in the bag after 30 min was removed using a large syringe and bubbled through NaOH to

trap the remaining $^{14}CO_2$, and the bag and putty was removed from the leaf.

3.3.3 Harvest, Dissection, and Counting Procedures.

Twenty-four hours after treatment with $^{14}CO_2$, plants (above-ground portion only) were taken from the field, senesced leaves and tillers were removed, and the remaining green portions were separated into the following parts: the treated leaf blades and sheaths, all other leaves, the inflorescence, the peduncle and penultimate internodes including the penultimate leaf node, the basal group of nodes/internodes to which tillers or tiller buds were attached, the remaining nodes/internodes, any tiller buds which were present, and any tillers which were present. The parts were dried at 90°C for 24 hours, cooled and stored in desiccators, weighed, then chopped finely.

Two subsamples weighing approximately 50-1000 mg were taken from the chopped material for each large plant part, depending on the anticipated activity. The subsamples, or all material from small plant parts, were oxidized using a biological oxidizer (Model B-306, Canberra Packard, Mississauga, Ontario). $^{14}CO_2$ was trapped in a scintillation cocktail containing Carbasorb CO_2 trapping agent (Canberra Packard, Mississauga, Ontario), PCS scintillant (Amersham, Oakville, Ontario), and xylene (CanLab, Winnipeg, Manitoba). Radioactivity was counted using a liquid scintillation counter (Model LS-1701, Beckman Instruments, Fullerton, California).

3.3.4 Statistical Techniques.

Data (dry weight and relative amount of radioactivity for each plant part) were subjected to SAS analysis of variance procedures (SAS Institute, 1982). Differences with $P<0.05$ were considered meaningful.

4. YIELD COMPONENTS AND NET GRAIN YIELD IN BARLEY TREATED WITH ETHEPHON.

4.1 Abstract.

Ethephon effectively reduces lodging in barley, but may also have positive or negative influences on grain yield and yield components even if lodging does not occur. The objective of this study was to investigate the effects of ethephon on yield and yield components of barley under western Canadian conditions. In 1987, 1988, and 1989, Argyle and Samson barley were grown at 100 and 300 plants m^{-2} and treated with ethephon at Zadoks growth stage 35 or 45. At harvest, grain yield samples were taken by hand or by combine, and yield components were determined from a sampling of plants from each plot. When lodging occurred, Belgian lodging indices were determined. Hand harvested grain yields were either unaffected or reduced by ethephon, but combine harvested yield tended to be increased by ethephon in 1989 when lodging was severe in untreated plots. Reductions in grain yield with ethephon treatment were related to reductions in kernels $spike^{-1}$ which occurred in all three years for barley grown at both plant densities. Ethephon increased spikes $plant^{-1}$ for barley grown at both 100 and 300 plants m^{-2} in 1987, which at the low plant density compensated for reductions in kernels $spike^{-1}$ and kernel weight. Barley in ethephon treated plots tended to be delayed in maturity compared with untreated plots. The potential for ethephon to cause yield reductions restricts the use of ethephon in western Canada to situations where the risk of severe lodging is high.

4.2 Introduction.

Ethephon applied to barley effectively reduces plant height and lodging. Grain yield has been reported to increase when ethephon has prevented lodging (Dahnous et al., 1982; Simmons et al., 1988), but positive and negative grain yield responses to ethephon have been reported even when no lodging had occurred in comparable untreated barley (Bahry, 1988; Caldwell et al., 1988; Danhous et al., 1982; Simmons et al., 1988).

Cereal grain yield can be thought of as the product of several components, namely, the average number of spikes per unit area, the average number of kernels per spike, and the average weight of individual kernels. The net effect of ethephon on grain yield then depends on the balance of positive, null, or negative responses of individual yield components to ethephon. Spikes $area^{-1}$ is reported to increase or be unaffected by ethephon application to barley (Bahry, 1988; Entz, 1988; Simmons et al., 1988). Kernels $spike^{-1}$ is decreased (Bahry, 1988; Simmons et al., 1988) or unaffected (Bahry, 1988; Entz, 1988; Simmons et al., 1988) by ethephon, and kernel weight is increased (Simmons et al., 1988), decreased (Bahry, 1988; Simmons et al., 1988), or unaffected (Bahry, 1988; Entz, 1988; Simmons et al., 1988). The most commonly reported responses are increases in spikes $area^{-1}$, and decreases in kernels $spike^{-1}$ and kernel weight.

Yield increases when ethephon prevented lodging of cereal crops have been attributed to increased kernel weight and/or increased harvestability due to the prevention of lodging (Brown and Earley, 1973; Cox and Otis, 1989; Dahnous et al., 1982; Foy and Witt, 1987; Hill et al., 1982; Simmons et al., 1988; Wiersma et al., 1986). Yield increases

with ethephon application in the absence of lodging have been attributed to increased spikes area^{-1} (Bahry, 1988; Hill et al., 1982). Yield decreases with ethephon application have been attributed to reduced kernels spike^{-1} (or panicle^{-1}) and/or reduced kernel weight (Bahry, 1988; Brown and Earley, 1973; Wunsche, 1977).

Factors which have been observed to influence the type and magnitude of yield component responses to ethephon include cultivar differences (Bahry, 1988; Dahnous et al., 1982; Entz, 1988; Simmons et al., 1988), ethephon application rate (Bahry, 1988; Dahnous et al., 1982; Entz, 1988; Simmons et al., 1988), crop growth stage at time of ethephon application (Brown and Earley, 1973; Caldwell et al., 1988), and environment (Entz, 1988; Simmons et al., 1988). Evidence presented by Bahry (1988) and Simmons et al. (1988) suggests that moisture availability during the growing season influences the response of spikes area^{-1} to ethephon application: increases in spikes area^{-1} which could compensate for reductions in kernel spike^{-1} and/or kernel weight tended to occur under conditions of greater growing season rainfall, whereas spikes area^{-1} tended not to be increased under drier conditions, often resulting in a net negative effect on grain yield.

The objective of this study was to determine the effect of ethephon application on net grain yield and on yield components under Manitoba conditions, with a view to more detailed examinations of specific yield component effects to be reported in subsequent chapters.

4.3 Materials and Methods.

Details of cultural practices and experimental design are given in chapter three. When lodging occurred, Belgian lodging indices (BLI) were determined. For yield component assessment at harvest, 40 plants in 1987 and 1988, and 10 plants in 1989 were sampled from the plot areas which had been thinned to the desired plant densities. Spikes $plant^{-1}$ was determined for each of these plants, then each spike was threshed using a single head thresher; the kernels from each spike were counted by hand then dried at 130°C for 21 hours (ASAE, 1987), grain weight $spike^{-1}$ was determined, and kernel weight was calculated. Bulk yield estimates were determined from hand harvests of a 1 m^2 area in all three seasons, and also from combine harvests of the center six rows of each plot in 1988 and 1989. In each case, the grain was cleaned and dried, then weighed.

From the late grain filling stage until harvest in 1989, periodic random harvests of 10 spikes were made from each cultivar, plant density, and ethephon treatment combination to monitor spike moisture content as a measure of relative maturity. Awns and the peduncle were trimmed off, then each spike was weighed, dried, and reweighed, and moisture was calculated in g kg^{-1}.

Analysis of variance was performed for each data set. Differences were considered meaningful if $P<0.05$. Simple correlation analyses were performed for control and ethephon treatment data combined, to give an indication of the effect of ethephon on the strength of relationships between the various yield, yield component, and lodging observations made.

4.4 Results.

Despite earlier evidence of differential responses between the two cultivars (Bahry, 1988; Entz, 1988), the two cultivars responded similarly to ethephon applications in all three years of this study. Cases where cultivar by ethephon treatment interactions were significant are noted in the text; otherwise, data presented are means over the two cultivars. Separate analyses of data for the two plant densities was often necessary because error variances were heterogeneous and/or because the plant density by ethephon treatment interactions were significant; therefore, for consistency of presentation, data from each plant density were analyzed separately.

Hand harvested grain yields were not increased by the application of ethephon, either being unaffected or reduced (Table 4.1). For barley grown at 100 plants m^{-2}, yield $plant^{-1}$ was not affected by ethephon application in 1987, but strong tendencies toward yield reductions were evident in 1988 and 1989 (P=0.07 and 0.06, respectively). Yield reductions due to ethephon application were common for yields calculated from hand harvested 1 m^2 samples, with the low plant density in 1987 and the high plant density in 1989 being the exceptions. For barley grown at 300 plants m^{-2} in 1988, the cultivar by ethephon treatment interaction was significant (P<0.05) for hand harvested samples because untreated Argyle yielded more than untreated Samson (453 and 421 g m^{-2}, respectively). In 1989, for barley grown at both densities, combine harvested grain yield appeared to be slightly increased (NS) by the application of ethephon, despite the reductions evident in the hand harvested samples. In general, application of ethephon to barley at GS

Table 4.1. Grain yield estimates for barley grown in the 1987, 1988, and 1989 seasons at two plant densities and with various ethephon treatments.

Ethephon Treatment	Individual Plant Sample$^{\Theta}$	Hand Harvested Bulk Sample$^{\Omega}$	Combine Harvested Bulk Sample$^{\Psi}$
	g plant^{-1}	g m^{-2}	kg ha^{-1}
		1987	
100 Plants m^{-2}			
Control	3.41 $^{\Phi}$	377	--
GS 35	3.49	375	--
GS 45	3.10	348	--
300 Plants m^{-2}			
Control	1.62	531 a	--
GS 35	1.47	477 ab	--
GS 45	1.32	443 b	--
		1988	
100 Plants m^{-2}			
Control	3.37 a	359 a	3650
GS 35	3.08 ab	332 ab	3410
GS 45	2.99 b	329 b	3230
300 Plants m^{-2}			
Control	1.25	437 a	3800
GS 35	1.16	372 b	3760
GS 45	1.12	383 b	3610
		1989	
100 Plants m^{-2}			
Control	6.29	557 a	5020
GS 45	5.39	476 b	5280
300 Plants m^{-2}			
Control	1.92	501	5150
GS 45	1.86	482	5420

$^{\Theta}$ Yield values given are means based on 40 plants selected for yield component analysis in 1987 and 1988, and on 10 plants selected for tillering observations and yield component analysis in 1989.
$^{\Omega}$ Yield values given are based on hand harvest of 1 m^2 in each plot.
$^{\Psi}$ Yield values given are based on combine harvests of centre 6 rows of each plot.
$^{\Phi}$ Yields are given at 0 g kg^{-1} moisture content. Means within a column of treatments in a particular year and at a particular plant density are significantly different if followed by different letters, based on LSD(0.05).

35 had an effect on grain yield that was intermediate to untreated barley and barley treated at GS 45.

Barley plants grown at 100 plants m^{-2} in 1989 had more spikes than those grown at the same density in 1988, which in turn had more spikes than those in 1987 (Table 4.2). Ethephon treatments to barley at both plant densities in 1987 increased the number of spikes $plant^{-1}$. In 1989, a similar trend was observed for both spikes m^{-2} and spikes $plant^{-1}$, although the increase approached significance (P=0.06) only for spikes m^{-2} at the low plant density.

Ethephon application caused reductions in kernels $spike^{-1}$ in all three years (Table 4.2). Plants not treated with ethephon had more kernels $spike^{-1}$ in 1987 and 1989 than in 1988, but the reductions caused by ethephon were greater in those years than in 1988. Ethephon applied at GS 45 caused a greater reduction in kernels $spike^{-1}$ than application at GS 35. Kernel weights were lower for barley treated with ethephon at both plant densities in 1987, while in 1988 and 1989, kernel weight was not influenced by ethephon application.

Belgian lodging indices (BLI) were variable in 1987 (coefficients of variation > 100); therefore, BLI's for barley treated with ethephon did not differ significantly from those for untreated barley (Table 4.2). In general, however, lodging was reduced by ethephon, barley grown at 300 plants m^{-2} lodged to a greater extent than barley grown at 100 plants m^{-2}, and Argyle barley lodged to a greater extent than Samson. In 1989, lodging in ethephon treated plots of both plant densities was clearly reduced compared to untreated plots. BLI's for Argyle barley were consistently higher than those for Samson, although

Table 4.2. Spike density, kernels spike^{-1}, kernel weight, and Belgian Lodging Index for barley grown in the 1987, 1988, and 1989 seasons at two plant densities and with various ethephon treatments.

Ethephon Treatment	Spike Density	Spike Density	Kernel Number	Kernel Weight	Belgian Lodging IndexΘ	
					Filling	Harvest
	m^{-2}	plant^{-1}	spike^{-1}	mg		
1987						
100 Plants m^{-2}						
Control	--	2.6 aΩ	46.7 a	28.8 a	0.6	2.1
GS 35	--	3.4 b	40.5 b	25.5 b	0.2	2.0
GS 45	--	3.8 b	35.1 c	23.7 b	0.3	0.8
300 Plants m^{-2}						
Control	--	1.3 a	41.3 a	29.7 a	1.7	2.6
GS 35	--	1.6 b	33.8 b	26.8 b	0.2	0.2
GS 45	--	1.7 b	29.9 b	27.0 b	0.2	1.9
1988						
100 Plants m^{-2}						
Control	304	3.1	40.4 a	26.8	--	--
GS 35	320	3.2	36.7 b	26.7	--	--
GS 45	312	3.1	35.4 b	27.5	--	--
300 Plants m^{-2}						
Control	382 a	1.2	37.7 a	27.2	--	--
GS 35	390 a	1.3	31.4 b	27.7	--	--
GS 45	365 b	1.2	32.7 b	28.4	--	--
1989						
100 Plants m^{-2}						
Control	341	3.9	50.2 a	31.9	1.5 a	3.9 a
GS 45	388	4.3	37.2 b	33.6	0.2 b	0.2 b
300 Plants m^{-2}						
Control	336	1.3	44.1 a	32.3	1.9 a	4.5 a
GS 45	374	1.5	38.4 b	31.9	0.2 b	1.2 b

Θ Belgian lodging indices given for barley during late grain filling period (July 16 and 24 in 1987 and 1989, respectively) and just prior to harvest (Aug. 4 in both 1987 and 1989).

Ω Means within a column of treatments in a particular year and at a particular plant density are significantly different if followed by different letters, based on LSD(0.05).

the cultivar by ethephon treatment interactions were not significant. No lodging occurred in 1988.

Using spike moisture content (awns and peduncle clipped off) as an indicator of relative maturity, barley treated with ethephon in 1989 matured later than untreated barley (Fig. 4.1). Cultivars and plant densities also tended to differ significantly from one another in spike moisture content; however, interactions between ethephon treatment and cultivar or plant density were not evident, with the exception of ethephon by plant density interactions on 26 and 29 days after ethephon application (P=0.03 and 0.02, respectively). These interactions arose because the differences in spike moisture content between treated and untreated barley were greater for barley grown at the low plant density than at the high plant density. A similar pattern was evident for later samplings, although in no other cases was the interaction statistically significant.

For barley grown at both 100 and 300 plants m^{-2} in 1987, spikes $plant^{-1}$ was negatively correlated with kernels $spike^{-1}$ (Table 4.3); this relationship was attributable to the opposite effects of ethephon on each of these components, with spikes $plant^{-1}$ being increased and kernels $spike^{-1}$ being decreased. Similarly, the positive correlation between kernels $spike^{-1}$ and kernel weight for barley grown at 100 plants m^{-2} was attributable to the positive effects of ethephon on each component. The positive correlations between kernels $spike^{-1}$ and yield for barley at 300 plants m^{-2} were indicative of the negative effect of ethephon on each. The negative relationship between spikes $plant^{-1}$ and kernel weight at both densities was partly attributable to opposite effects of ethephon on each component; however, for barley grown at the

Fig. 4.1. Decline of spike moisture content during late grain filling to maturation period for ethephon treated and untreated barley grown in 1989.

Note: Ethephon was applied at Zadoks GS 45, which occurred on June 29. Each point is a mean of moisture contents for 40 individual spikes.

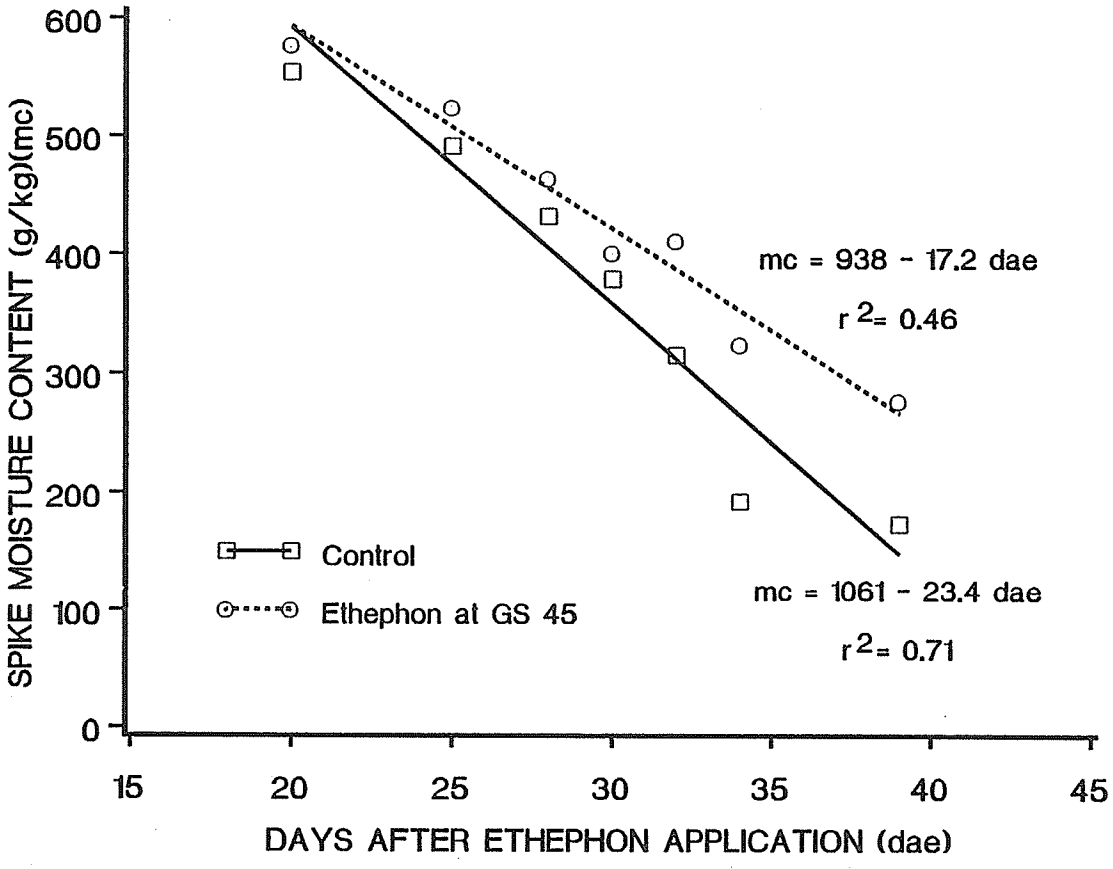

SPIKE MOISTURE CONTENT (g/kg)(mc)
600
500
400
300
200
100
0
15
20
25
30
35
40
45
DAYS AFTER ETHEPHON APPLICATION (dae)
mc = 938 - 17.2 dae
r 2= 0.46
mc = 1061 - 23.4 dae
r 2= 0.71
Control
Ethephon at GS 45

Table 4.3. Simple correlation coefficients for various yield and yield component observations made in the 1987 growing season for barley grown at two planting densities; analysis performed for control and ethephon treatment data combined.

Variables	Spikes plant^{-1}	Kernels spike^{-1}	Kernel weight	Yield plant^{-1}Θ	Yield m^{-2}Ω	Lodging Indices Jul 16	Jul 24
			100 Plants m^{-2}				
Kernels spike^{-1}	-0.53**						
Kernel weight	-0.83**	0.52**					
Yield plant^{-1}Θ	0.57**	0.28	-0.21				
Yield m^{-2}Ω	0.52**	0.32	-0.20	0.95**			
Lodging Indices							
Jul 16	0.07	0.13	-0.03	0.26	0.28		
Jul 24	0.07	0.37	-0.11	0.39	0.41*	0.74**	
Aug 4	0.19	0.30	-0.29	0.38	0.34	0.47*	0.86**
			300 Plants m^{-2}				
Kernels spike^{-1}	-0.63**						
Kernel weight	-0.63**	0.23					
Yield plant^{-1}Θ	-0.11	0.69**	0.31				
Yield m^{-2}Ω	-0.12	0.67**	0.35	0.98**			
Lodging Indices							
Jul 16	-0.13	0.24	0.00	0.19	0.11		
Jul 24	-0.22	0.33	-0.04	0.15	0.11	0.67**	
Aug 4	0.07	0.14	-0.21	0.06	0.05	0.54**	0.88**

*,** Simple correlation coefficient significant at P=0.05 and 0.01, respectively.
Θ Yield estimate based on sample of 40 plants.
Ω Yield estimate based on hand harvest of 1 m^2.

low plant density such a relationship was also evident when the analysis was performed separately for each ethephon treatment (r=-0.70 and -0.88 for control and ethephon at GS 45 treatments, respectively), indicating a more general relationship between these two yield components, regardless of ethephon treatment. Spikes plant^{-1} for barley at 100 plants m^{-2} was positively correlated with yield plant^{-1}; a plot of the data revealed that the correlation could be attributed to non-significant cultivar differences, with Samson having slightly more spikes plant^{-1} and greater yield plant^{-1} than Argyle.

Negative correlations between spikes plant^{-1} and/or m^{-2} and kernel weight at either plant density in 1988 (Table 4.4) suggest a general inverse relationship between these components, since ethephon affected neither. The positive relationships between spikes plant^{-1} or m^{-2} and the hand-harvested yield estimates for barley grown at the low density, and between spikes plant^{-1} and yield plant^{-1} at the high density were found to be attributable to the slightly but non-significantly higher spikes and yield plant^{-1} of Samson, and to a general trend towards increased yield with increased spikes plant^{-1}. The positive correlations between kernels spike^{-1} and the various yield estimates at both plant densities could be attributed to the negative effect of ethephon on both kernels spike^{-1} and net grain yield. Combine harvestable yield (yield ha^{-1}) was correlated with both hand harvested yield estimates (yield plant^{-1} or m^{-2}) at $P<0.06$ for barley grown at 300 plants m^{-2}.

The relationships between spikes plant^{-1} or m^{-2} and kernels spike^{-1} at both densities in 1989 (Table 4.5) reflect the opposite effects of ethephon on each component. The negative relationship

Table 4.4. Simple correlation coefficients for various yield and yield component observations made in the 1988 growing season for barley grown at two planting densities; analysis performed for control and ethephon treatment data combined.

Variables	Spikes plant^{-1}	Spikes m^{-2}	Kernels spike^{-1}	Kernel weight	Yield plant^{-1}Θ	Yield m^{-2}Ω
			100 Plants m^{-2}			
Spikes m^{-2}	0.82**					
Kernels spike^{-1}	0.25	0.00				
Kernel weight	-0.52**	-0.44*	-0.24			
Yield plant^{-1}Θ	0.65**	0.40*	0.78**	-0.08		
Yield m^{-2}Ω	0.71**	0.53**	0.57**	-0.21	0.83**	
Yield ha^{-2}Ψ	-0.00	-0.09	0.52**	-0.14	0.34	0.18
			300 Plants m^{-2}			
Spikes m^{-2}	0.37					
Kernels spike^{-1}	-0.34	0.00				
Kernel weight	-0.02	-0.41*	-0.04			
Yield plant^{-1}Θ	0.51**	0.16	0.56**	0.24		
Yield m^{-2}Ω	-0.31	0.09	0.85**	-0.30	0.37	
Yield ha^{-2}Ψ	0.30	0.34	0.28	-0.23	0.40*	0.39

*,** Simple correlation coefficient significant at P=0.05 and 0.01, respectively.
Θ Yield estimate based on sample of 40 plants.
Ω Yield estimate based on hand harvest of 1 m^2.
Ψ Yield estimate based on combine harvest of 1.2 x 7.5 m strip.

Table 4.5. Simple correlation coefficients for various yield and yield component observations made in the 1989 growing season for barley grown at two planting densities; analysis performed for control and ethephon treatment data combined.

Variables	Spikes plant^{-1}	Spikes m^{-2}	Kernels spike^{-1}	Kernel weight	Yield plant^{-1}Θ	Yield m^{-2}Ω	Yield ha^{-1}Ψ	Lodging Jul 24
			100 Plants m^{-2}					
Spikes m^{-2}	0.81**							
Kernels spike^{-1}	-0.47	-0.57*						
Kernel weight	0.10	0.11	-0.33					
Yield plant^{-1}Θ	0.37	0.14	0.56*	0.15				
Yield m^{-2}Ω	0.32	0.27	0.58*	-0.06	0.90**			
Yield ha^{-1}Ψ	0.45	0.51*	-0.30	0.05	0.08	0.19		
Lodging Indices								
Jul 24	-0.02	-0.22	0.55*	-0.26	0.49*	0.55*	-0.38	
Aug 4	-0.26	-0.57*	0.83**	-0.46	0.49*	0.51*	-0.43	0.78**
			300 Plants m^{-2}					
Spikes m^{-2}	0.65**							
Kernels spike^{-1}	-0.77**	-0.63*						
Kernel weight	-0.55*	-0.47	0.20					
Yield plant^{-1}Θ	0.45	0.32	-0.18	0.31				
Yield m^{-2}Ω	0.09	0.33	-0.16	0.40	0.53*			
Yield ha^{-1}Ψ	0.41	0.41	-0.57*	-0.33	-0.06	0.24		
Lodging Indices								
Jul 24	0.14	0.01	0.24	-0.52*	-0.03	0.09	-0.34	
Aug 4	-0.08	-0.34	0.46	-0.39	-0.12	-0.13	-0.24	0.66**

*,** Simple correlation coefficient significant at P=0.05 and 0.01, respectively.
Θ Yield estimate based on sample of 40 plants.
Ω Yield estimate based on hand harvest of 1 m^2.
Φ Yield estimate based on combine harvest of 1.2 x 7.5 m strip.

between spikes plant^{-1} and kernel weight at the high plant density suggested a general relationship, since neither component was significantly affected by ethephon. For barley grown at 100 plants m^{-2}, spikes m^{-2} was negatively correlated with harvestable yield (yield ha^{-1}) because of the tendency for both to be increased by ethephon. Kernels spike^{-1} was positively correlated with hand harvested yield estimates (yield plant^{-1} and m^{-2}) at the low density, but negatively correlated with combine harvestable yield (yield ha^{-1}) at the high density. The former cases reflect the negative effects of ethephon on both kernels spike^{-1} and absolute grain yield, while the latter is attributable to the tendency for harvestable grain yield to increase with ethephon application despite the decrease of kernels spike^{-1}. Hand harvested grain yield estimates were not correlated with the combine harvested yield estimate.

Aside from the positive correlation between spikes plant^{-1} and Belgian lodging index (BLI) on July 24 for barley grown at 100 plants m^{-2}, BLI was not closely related with yield or yield components in 1987 at either plant density (Table 4.3). For barley grown at 100 plants m^{-2} in 1989, positive correlations were found between BLI on either observation date and each of yield plant^{-1}, yield m^{-2}, and kernels spike^{-1} (Table 4.5). The negative relationship between BLI on August 4 and combine harvested yield approached significance (P=0.09). Spikes m^{-2} was negatively correlated with BLI on August 4. Lodging indices for barley grown at 300 plants m^{-2} were not correlated with yield or with spikes plant^{-1} or m^{-2}; kernel weight was negatively correlated with BLI on July 24, and the correlation between kernels spike^{-1} and BLI on August 4 approached significance (P=0.08).

Generally, yield and yield component estimates based on 10 plants plot^{-1} were positively correlated with estimates based on 40 plants plot^{-1} (Table 4.6), with the estimates of spikes plant^{-1} in 1988 being the only exception.

4.5 Discussion.

Absolute grain yields, estimated from either a sampling of plants or from a harvest of a 1 m^2 area, were in no case increased by ethephon application whether or not lodging occurred. Barley grain yield increases with ethephon application have been reported when lodging was reduced (Dahnous et al., 1982; Simmons et al., 1988), but have also been reported in cases where no lodging occurred (Bahry, 1988). Because lodging was relatively severe on untreated plots in 1989, ethephon tended to increase combine harvested grain yields, despite the decreased absolute grain yield on the same plots.

Grain yield is the product of the components spikes area^{-1}, kernels spike^{-1} and kernel weight. While increases in spikes area^{-1} with ethephon application are commonly reported (Bahry, 1988; Entz, 1988; Simmons et al., 1988), in this study, spikes plant^{-1} (equivalent to spikes area^{-1} given the uniform plant densities) increased significantly only in 1987. Evidence presented in chapter five shows that ethephon promoted the emergence of tillers after GS 45 in both 1987 and 1989. In 1987, this resulted in more spikes plant^{-1} on treated barley compared with untreated. In contrast, ethephon had no apparent effect on spikes plant^{-1} in 1989 because ethephon promoted both emergence of tillers after GS 45 and senescence of some tillers which had emerged prior to ethephon application. The resumption of tillering after heading of cereal plants appears to be enhanced by adequate

Table 4.6. Simple correlation coefficients for yield component estimates based on samples of 40 and 10 plants plot^{-1} for barley grown in 1987 and 1988.

Variable	Growing Season 1987	1988
	100 Plants m^{-2}	
Spikes plant^{-1}	0.88**⊖	0.19
Kernels spike^{-1}	0.83**	0.82**
Kernel weight	0.89**	0.68**
Yield Plant^{-1}	0.63**	0.61**
	300 Plants m^{-2}	
Spikes plant^{-1}	0.74**	0.01
Kernels spike^{-1}	0.78**	0.61**
Kernel weight	0.75**	0.49*
Yield Plant^{-1}	0.68**	0.42*

⊖ Each coefficient is for the correlation between estimates of the specific yield component based on 40 and 10 plants plot^{-1}.

moisture (Kirby, 1967), so the effect of ethephon on late tillering may depend on the presence of favourable levels of moisture. Growing season rainfall in 1987 and 1989 was considerably higher than in 1988, suggesting that adequate moisture conditions are necessary for the promotion of late tillering by ethephon (potentially leading to increased spikes plant^{-1}).

Ethephon application consistently resulted in fewer kernels spike^{-1} on treated plants compared with untreated plants. Two factors contributed to this reduction in kernels spike^{-1} for plants treated with ethephon: an apparent reduction caused by the presence of shoots which first appeared after GS 45 and had relatively low numbers of kernels spike^{-1}, and an actual reduction on main stems and early tillers (chapter six). This actual reduction in kernels spike^{-1} may be due to previously observed gametocidal properties of ethephon (Stoskopf and Law, 1972).

Like the reduction of kernels spike^{-1}, the reductions of kernel weight by ethephon application in 1987 at both densities also had apparent and actual components (chapter six). The actual reductions in kernel weight may be attributable to competition for photosynthetic assimilates, since shoots which appeared after ethephon was applied would initially be dependent on assimilates from the main stem, a dependence which could be in competition with the developing main stem inflorescence (chapter seven). The consistent negative correlation between spikes plant^{-1} and kernel weight may also be reflective of competition between plant parts. The potentially positive effect of ethephon on spikes plant^{-1} did not compensate for negative effects of ethephon on kernels spike^{-1} and kernel weight.

The release of ethylene from ethephon is enhanced with increased temperatures (Lougheed and Franklin, 1972; Olien and Bukovac, 1978). One might then reason that relatively high temperatures during the period following ethephon application (as ethylene is released from ethephon) may exacerbate the negative effect of ethephon on kernels spike^{-1}. The magnitude of the reduction in kernels spike^{-1} for barley grown at 300 plants m^{-2} in 1987 was substantially larger than that for comparable barley in 1989, and temperatures for the 7 day period following ethephon application were higher in 1987 than in 1989 (respectively, maximum and mean maximum daily temperatures were 33.7 and 29.1^{o}C in 1987, compared with 31.6 and 26.8^{o}C in 1989). However, a similar trend was not evident for barley grown at 100 plants m^{-2} in those years, suggesting that temperatures during the period when ethephon was being released did not have a major influence on the reduction of kernels spike^{-1}.

Increases in plant density may increase grain yield due to increased spikes area^{-1}, despite decreases in spikes plant^{-1} and kernels spike^{-1} (Kirby, 1967). In 1987 and 1988, such increases in grain yield with increased plant density were evident; in 1989, grain yield was reduced with increased plant density, apparently because spikes m^{-2} did not increase with plant density. Neither in yield nor in kernels spike^{-1} were reductions due to ethephon application consistently larger or smaller for one plant density over the other. Therefore, despite the greater responsiveness of plants at the low density to ethephon in terms of promoted tillering, it cannot be concluded that higher or lower plant densities have advantages with respect to the likelihood of negative yield responses to ethephon application. A grower's choice of planting

density then depends on optimizing grain yield irrespective of responsiveness to ethephon; the optimum density in these studies was nearer 300 plants m^{-2} in 1987 and 1988, suggesting that in southern Manitoba, densities of this order are more likely to optimize grain yield than densities near 100 plants m^{-2}.

Application of ethephon for lodging control is assumed most effective during the boot stage (GS 41-47)(Brown and Early, 1973), and the boot stage is the recommended time of application. The application at GS 35 was generally less detrimental to yield in the current studies, while the sporadic lodging in 1987, and the absence of the treatment in 1989, make conclusions as to the effectiveness of the earlier application compared with the later application for lodging control impossible. Caldwell et al. (1988) reported lodging control with application at GS 37 to be equal to or better than with application at GS 45. Earlier application of ethephon may possibly provide equal lodging protection with less detriment to yield than later application under Western Canadian conditions.

The correlation analyses were conducted to examine the effect of ethephon on the relationships among yield components and yield. Plant densities were analyzed separately, and generally no significant cultivar effects occurred; therefore, aside from random variation and any non-significant cultivar trends, the remaining variation is primarily attributable to the effect of ethephon on either one or both of the sets of data being considered.

Spikes $plant^{-1}$ was negatively correlated with kernels $spike^{-1}$ in 1987 and 1989 at both plant densities because ethephon increased spikes $plant^{-1}$ while it decreased kernels $spike^{-1}$. Kernels $spike^{-1}$ was

positively correlated with hand harvested yield estimates for barley grown at the high density in 1987, both densities in 1988, and the low density in 1989, because both were decreased with ethephon application. These results imply that the consistent reductions in kernels spike^{-1} caused by ethephon pose a considerable risk to yield in the absence of positive effects of ethephon on spikes plant^{-1}.

The negative correlations which occurred consistently between spikes plant^{-1} and kernel weight (except at 100 plants m^{-2} in 1989) could only partly be explained by ethephon effects. Such correlations were evident in cases when ethephon exerted no significant influence on either component, and in cases where ethephon did influence the components (as in 1987), the correlations were significant even when the analyses were performed separately for each ethephon treatment, indicating a general inverse relationship between spikes plant^{-1} and kernel weight regardless of ethephon treatment.

Combine harvested yield estimates were generally poorly correlated with hand harvested yield estimates, although some correlation was evident for barley grown at the high plant density in 1988 when no lodging occurred. The lack of correlation between these yield estimates in 1989 can be attributed to the lodging which occurred in plots not treated with ethephon. For hand harvested yield estimates (expressed as yield plant^{-1} or m^{-2}) all grain for a number of plants or a certain area was harvested, giving a measure of absolute grain yield; during combine harvesting, not all of the lodged barley could be picked with the combine, thus the combine harvested yield estimate (expressed as yield ha^{-1}) gives a measure of harvestable grain yield.

Lodging was sporadic in 1987, resulting in high statistical variability and the inability to detect differences between ethephon treated and untreated barley. Due to increased exposure to wind, lodging was more severe in border blocks regardless of whether or not individual plots within the block were treated with ethephon. Because poor emergence made it necessary to modify the experiment to a completely randomized design, significant block effects could not be detected and removed from the error sum of squares, hence contributing to the inability to detect ethephon treatment differences. The lack of correlation between yield and BLI in 1987 was probably due to the high variability in lodging scores. In 1989, lodging also occurred, and ethephon treatment clearly reduced lodging. BLI showed some negative correlation with kernel weight, consistent with other reports (Pinthus, 1973). The positive correlations between BLI and kernels spike^{-1} for barley grown at 100 plants m^{-2}, and to a lesser extent at 300 plants m^{-2} result from reductions in both BLI and kernels spike^{-1} with ethephon application. This implies that lodging resistance in ethephon treated barley is conferred not only by shortened (Brown and Early, 1973; Entz, 1988; Neenan and Spencer-Smith, 1975) and possibly strengthened (Selga et al., 1985) stems, but also by the reduced weight often carried on stems, since any factor which decreases the force applied to a cereal stem will decrease the tendency to lodge (Neenan and Spencer-Smith, 1975).

The strong correlations between estimates of yield and yield components based on 40 or 10 plants plot^{-1} in 1987 and 1988 provided justification for a decision to use only estimates based on 10 plants plot^{-1} in 1989. Only the 40 and 10 plant estimates of spikes plant^{-1} in

1988 were not correlated with one another, possibly due to relatively dry conditions not conducive to tillering.

The maturity delay caused by ethephon in 1989 appeared to be due more to the late tillers which emerged and produced spikes after ethephon application than to maturity delays for main stems and early formed tillers; therefore, maturity within the treated crop was less uniform than in the untreated crop. The greater spike to spike variability in moisture content, and hence in maturity, accounts for the lower R^2 for the regression of moisture content with time for treated barley as displayed in Fig. 4.1. A similar delay in maturity when barley was treated with ethephon was visually observed in 1987, but to a much lesser extent in 1988 when very few tillers emerged after ethephon application. Others have observed delays in maturity with the application of ethephon to barley (Pearson et al., 1989). Such delays in maturity may pose harvesting problems if maturity of late tillers is delayed to such an extent that grain on main stems and early tillers becomes excessively dry, yet the late tillers which cause the maturity delay provide necessary compensation for the negative effects of ethephon on kernels spike^{-1} and kernel weight.

Ethephon reduced lodging in 1989, and less conclusively so in 1987. Lodging was severe in untreated plots in 1989 and combine harvestable yields in ethephon treated plots tended to be higher than in untreated plots, despite reductions in absolute grain yield. However, reductions in kernels spike^{-1} were caused by the application of ethephon in all three years, which often resulted in decreased grain yield. Apparently under conditions of adequate moisture, ethephon caused increases in spikes plant^{-1}, but this rarely compensated for the loss of

kernels spike^{-1}. Such increases in spikes plant^{-1} also contributed to delayed maturity of the crop. The risks associated with the use of ethephon to reduce lodging of barley under Canadian Prairie conditions make it imperative that a choice to use ethephon be based on knowledge of current environmental conditions and the likelihood of severe lodging.

5. TILLERING PATTERN AND ITS IMPACT ON YIELD IN BARLEY TREATED WITH ETHEPHON.

5.1 Abstract

Ethephon used for lodging protection in barley often increases spikes m^{-2}. This study was undertaken to determine the effects of ethephon on tiller emergence and survival, as well as to determine the significance with respect to yield of additional spikes appearing on ethephon treated barley plants. Ethephon was applied at a rate of 240 g ha^{-1} to Argyle and Samson barley grown at 100 and 300 plants m^{-2}; applications were made at Zadoks GS 35 and 45 in 1987 and 1988, and at GS 45 in 1989. Ten plants $plot^{-1}$ were observed at intervals through the growing seasons; tillers were tagged as they emerged and their contributions to spikes $plant^{-1}$ and grain yield were determined at harvest. The two cultivars responded to ethephon applications similarly with respect to tillering and yield. After ethephon applications, shoots $plant^{-1}$ increased on treated plants compared with untreated plants grown at both plant densities in all three years. Application at Zadoks GS 45 increased shoots $plant^{-1}$ more than application at GS 35 in 1987 when moisture was adequate, but less in 1988 when some moisture stress may have affected barley more at the second application time than at the first application time. Late appearing shoots contributed to spikes $plant^{-1}$ and grain yield $plant^{-1}$ for both plant densities in 1987, and for the low plant density in 1989, but total yield $plant^{-1}$ was often decreased and was never increased by the application of ethephon. Any increases in spikes $plant^{-1}$ due to ethephon application were attributable to late tiller production and survival rather than to prevention of senescence of early formed tillers.

5.2 Introduction.

The growth regulator ethephon [(2-chloroethyl)phosphonic acid] has been successfully used to enhance the lodging resistance of cereal crops, which it accomplishes in part by restricting the degree to which stems elongate. When lodging is prevented by the application of ethephon, harvestable grain yield increases may result (Dahnous et al., 1982; Simmons et al., 1988). In addition to reducing lodging, ethephon applied to cereals may influence yield by affecting individual yield components either positively or negatively. Decreases in kernels spike^{-1} and kernel weight have commonly been observed (Bahry, 1988; Simmons et al., 1988; Wunsche, 1977). Increases in spikes m^{-2} have been reported for spring barley (Bahry, 1988; Entz, 1988; Morena et al., 1988; Simmons et al., 1988), winter barley (Hill et al., 1982), and wheat (Simmons et al., 1988) treated with ethephon. Cases in which ethephon had no effect on spikes area^{-1} are also common, but reports of decreases in spikes area^{-1}, such as that of Cox and Otis (1989) for winter wheat, are uncommon. Increases in spikes m^{-2} have been associated with grain yield increases in the absence of lodging (Bahry, 1988, Hill et al., 1982).

During barley development, shoot number increases during the tillering phase to a maximum early in the stem elongation phase (Gallagher et al., 1976; Simmons et al., 1982). Some of these tillers may senesce, resulting in some final number of grain-bearing shoots. Tiller emergence sometimes resumes after heading (Aspinall, 1961; 1963; Kirby, 1967). Johnston and Jeffcoat (1977) attributed suppressed growth and emergence of tiller buds during rapid stem elongation to competition for photosynthetic assimilates in favour of the elongating stem; tiller

emergence could resume when the flag leaf became the primary supplier for the developing inflorescence, relieving the competition for assimilates at bud sites. Plant growth substances such as auxin, cytokinin, and ethylene likely also play interacting roles in the growth of tiller buds (Harrison and Kaufman, 1980; 1984).

Ethephon is normally applied to barley during the boot stage (Zadoks GS 39 to 45), during the time when many tillers may be senescing; therefore, it has been suggested that ethephon enhances the survival of tillers which might otherwise senesce, thereby increasing spikes m^{-2} (Bahry, 1988; Morena et al., 1988; Simmons et al., 1988). However, ethephon has also been known to promote the appearance of late tillers (Hill et al., 1982; Netherlands, 1989), and the significance of these with respect to final spike number and grain yield is unknown.

The objectives of this study were, first, to determine whether increases in spikes $plant^{-1}$ or m^{-2} observed with ethephon application could be attributed to the prevention of senescence of early tillers or the promotion of emergence of late tillers, and second, to determine the significance of the additional spikes with respect to yield.

5.3 Materials and Methods.

Details of cultural methods and experimental design are given in chapter three. Ten plants were randomly selected within the plot areas which had been thinned to the desired plant densities. At intervals of two to eleven days, depending on how rapidly tillers were emerging, tillers emerged from their subtending leaf sheaths were labelled with colour-coded wire loops, and the date of emergence was recorded. In cases where a tiller was emerged but not yet large enough on which to place a wire loop, the date was recorded and the wire loop was placed on

the tiller at a later date. The colour-coding of wire loops conformed to the tiller characterization system of Klepper et al. (1982). When a tiller senesced, the date when senescence was first observed was recorded; senescence of the youngest leaf on a tiller was taken as a sign of tiller senescence.

At harvest, each spike from each of the 10 plants being observed was individually threshed using a single head thresher/cleaner. Spikes plant^{-1} and grain weight spike^{-1} were determined. From the latter, yields spike^{-1} and plant^{-1} were determined. Spikes were categorized according to the time when the tiller had first emerged, so that the contributions of early (before ethephon application) and late (after ethephon application) tillers to spikes plant^{-1} and grain yield plant^{-1} could be determined.

In 1988 and 1989, ten plants were sampled from each cultivar and plant density combination at GS 45. These plants were dissected and the locations (according to the tiller characterization system being used) of each emerged tiller and each non-emerged tiller bud were recorded.

Analysis of variance of shoots plant^{-1} was performed for each date when observations were made, and also for spikes plant^{-1} and grain yield plant^{-1}. Differences were considered meaningful at $P<0.05$.

5.4 Results.

Shoots plant^{-1} observed at intervals through each of the growing seasons are presented in Fig.'s 5.1-5.3. Generally, the two cultivars displayed similar patterns of tiller emergence, senescence, and survival and did not respond differently to ethephon application, therefore the data presented are means over the two cultivars unless otherwise noted. Plants not treated with ethephon displayed a typical pattern of tiller emergence and senescence, with shoots plant^{-1} increasing to a maximum, then falling off as tiller senescence became apparent after the boot stage. Very few new tillers emerged after heading for plants not treated with ethephon. More tillers appeared on plants grown at 100 plants m^{-2} than on those grown at 300 plants m^{-2}, because the tillering phase extended several days longer for barley grown at the lower density.

For plants grown at 100 plants m^{-2}, ethephon at either GS 35 or 45 increased shoots plant^{-1} after the time of application in all three years (Fig.'s 5.1-5.3). In 1987, ethephon application at GS 45 increased shoots plant^{-1} more than application at GS 35 (Fig. 5.1). In contrast, treatment with ethephon at GS 35 in 1988 promoted shoots plant^{-1} more than treatment at GS 45 (Fig. 5.2). Increased spikes plant^{-1} were present at harvest for barley treated with ethephon only in 1987 (Fig. 5.1).

In 1989, evidence of cultivar by ethephon interactions emerged in the analyses of shoots plant^{-1} for days 55 and 63 (P=0.02 and 0.06, respectively). On these days, the difference between shoots plant^{-1} for control and treated Argyle barley was greater than for Samson barley (Fig. 5.4). The interaction was not significant at harvest, although

Fig. 5.1. Shoots plant^{-1} over the 1987 growing season for barley grown at two plant densities with various ethephon treatments.

Note: Ethephon was applied at 32 and 34 days after plant emergence for GS 35 and 45 treatments, respectively. F-test for ethephon application significant at $P<0.05$ for observations on days 40-87 for both plant densities.

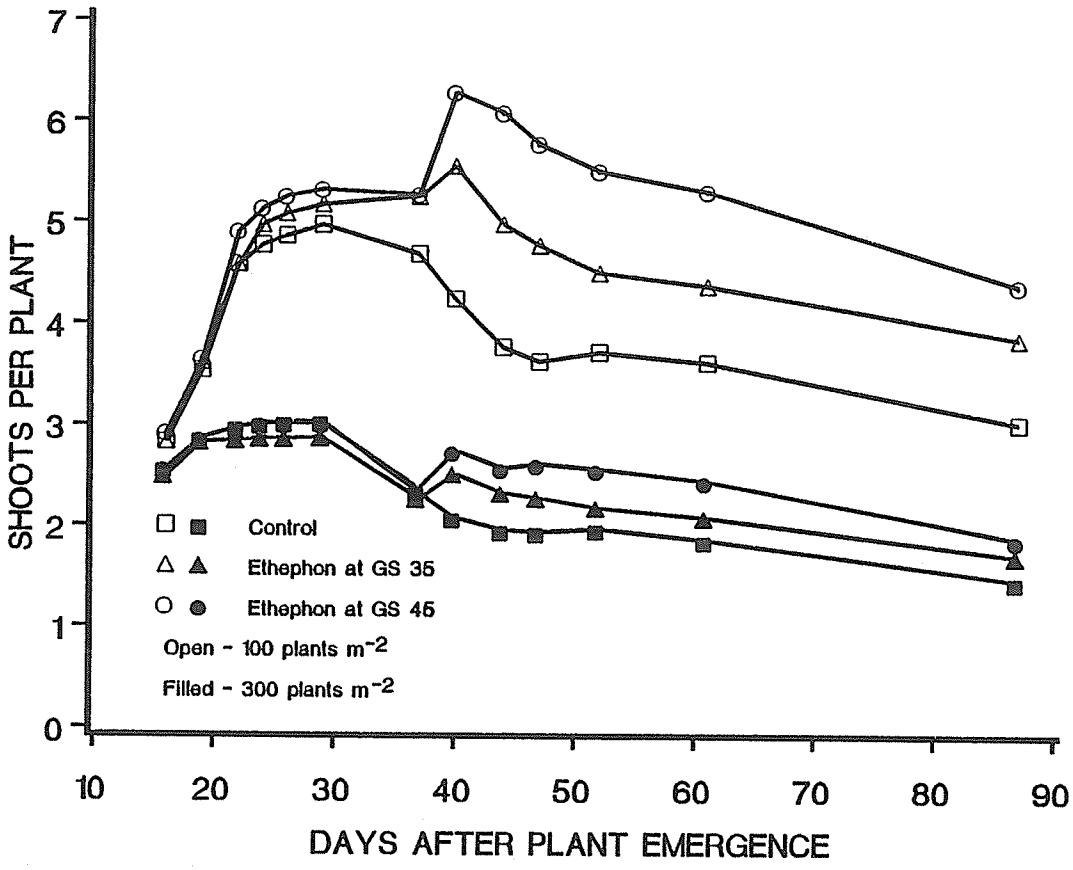

SHOOTS PER PLANT
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE
Control
Ethephon at GS 35
Ethephon at GS 45
Open - 100 plants m-2
Filled - 300 plants m-2

Fig. 5.2. Shoots plant^{-1} over the 1988 growing season for barley grown at two plant densities with various ethephon treatments.

Note: Ethephon was applied at 30 and 34 days after plant emergence for GS 35 and 45 treatments, respectively. F-test for ethephon application significant at $P<0.05$ for observations on days 38-54, and 47-61 for barley grown at 100 and 300 plants m^{-2}, respectively.

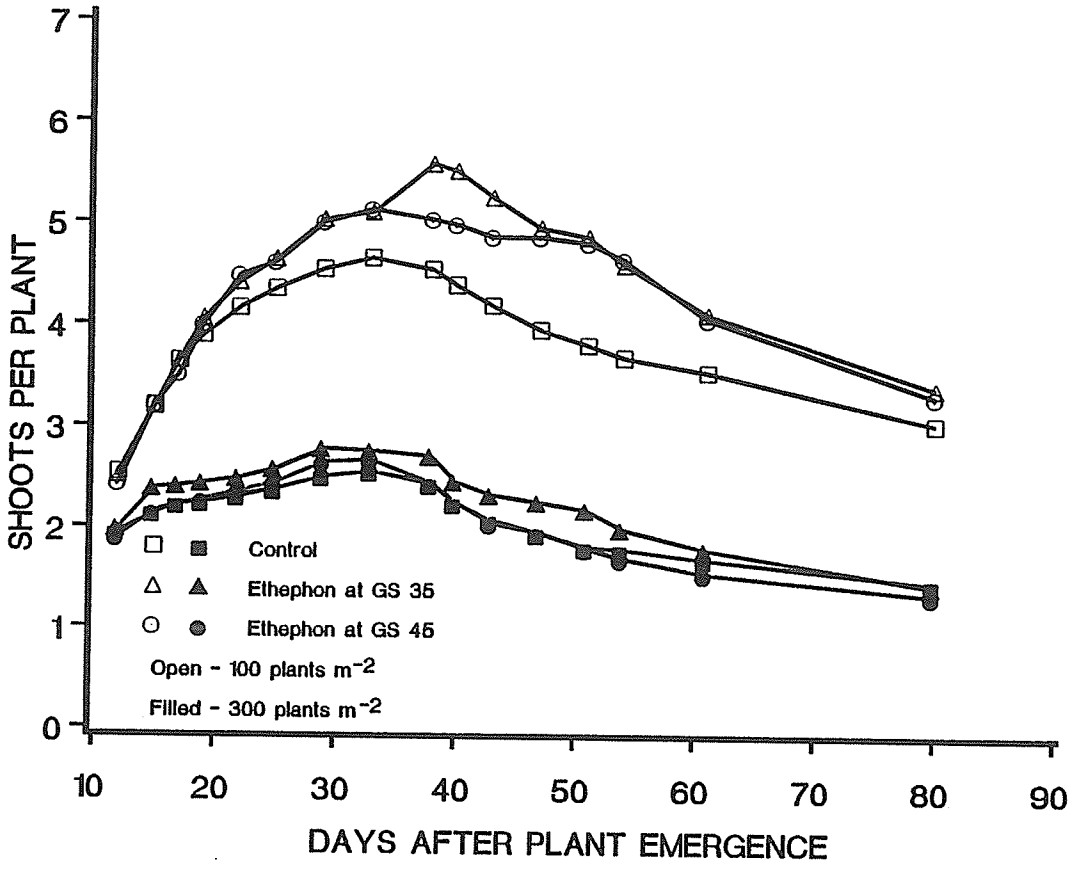

SHOOTS PER PLANT
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE
Control
Ethephon at GS 35
Ethephon at GS 45
Open - 100 plants m-2
Filled - 300 plants m-2

Fig. 5.3. Shoots plant^{-1} over the 1989 growing season for barley grown at two plant densities with various ethephon treatments.

Note: Ethephon was applied at 39 days after plant emergence for GS 45 treatment. F-test for ethephon application significant at $P<0.05$ for observations on days 49 through 63 for both plant densities.

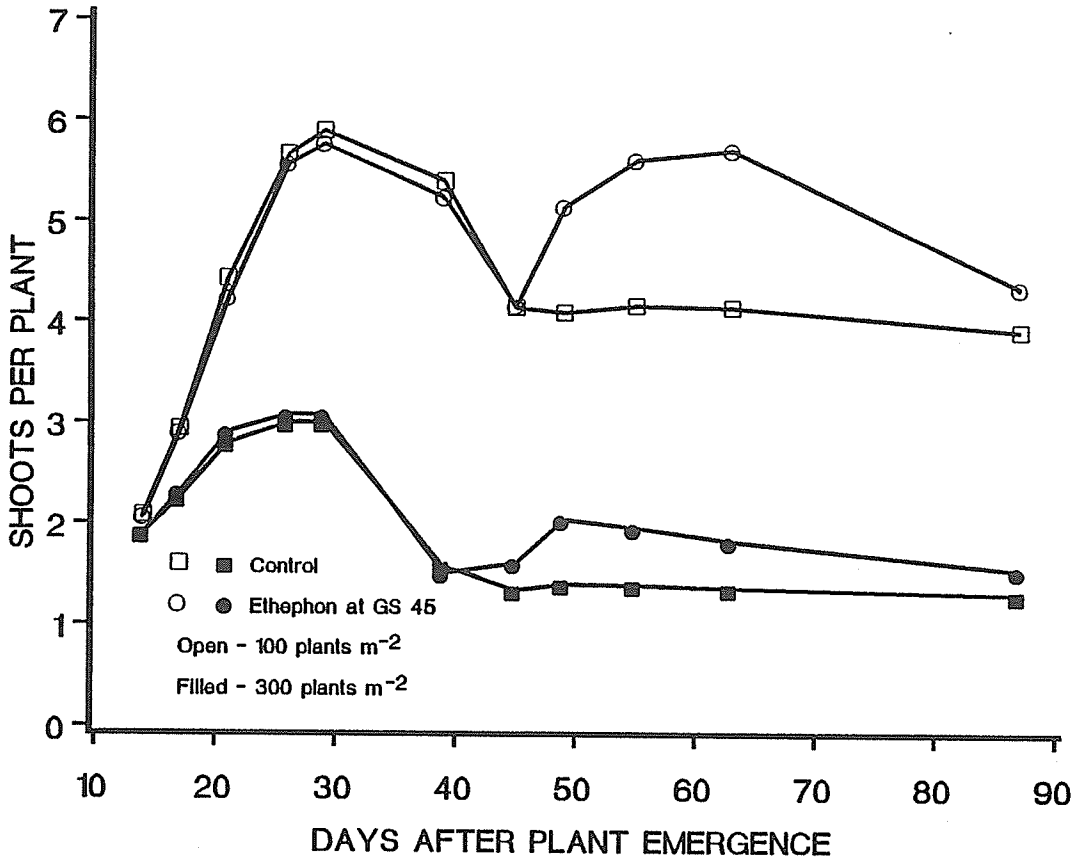
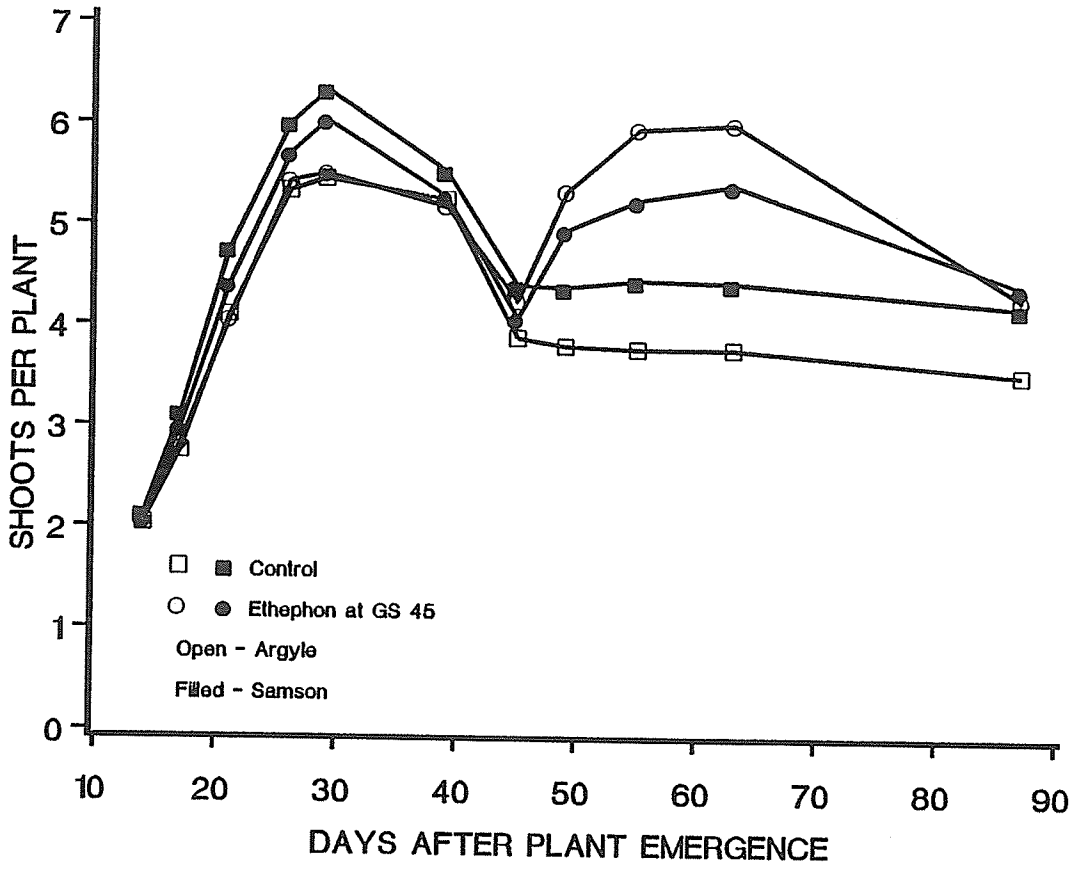

SHOOTS PER PLANT
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE
Control
Ethephon at GS 45
Open - 100 plants m-2
Filled - 300 plants m-2

Fig. 5.4. Shoots plant^{-1} over the 1989 growing season for Argyle and Samson barley grown at 100 plants m^{-2} with various ethephon treatments.

Note: Ethephon was applied at 39 days after plant emergence for GS 45 treatment. F-test for ethephon application significant at $P<0.05$ for observations on days 49 through 63 for both plant densities.


SHOOTS PER PLANT
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE
Control
Ethephon at GS 45
Open - Argyle
Filled - Samson

treated Argyle plants had slightly more spikes than untreated, while treated and untreated Samson plants had equal spike numbers. In contrast, Samson tended to produce more late tillers than Argyle at 100 plants m^{-2} in 1987, although the interaction was not significant.

The responses for barley grown at 300 plants m^{-2} were similar to those observed for barley grown at 100 plants m^{-2}, but smaller in magnitude (Fig.'s 5.1-5.3). Ethephon application increased shoots $plant^{-1}$, but increased spikes $plant^{-1}$ occurred only in 1987.

Tillers arising from specific locations on the plant made similar contributions to total shoots $plant^{-1}$ for plants not treated with ethephon in all three years (Fig.'s 5.5-5.10). During the tillering phase of barley grown at 100 plants m^{-2} (Fig.'s 5.5-5.7), tillers 1, 2, and 3 were produced by most plants, and a large proportion of these tillers survived to bear grain. Many plants also produced tiller 10, but the rate of survival was low. In 1987 and 1989, a few plants produced tillers 11, 20, and 4 during the tillering phase, while the coleoptile tiller (0), appeared on a few plants only in 1988 and 1989. During the tillering phase of barley grown at 300 plants m^{-2} (Fig.'s 5.8-5.10), most plants produced tillers 1 and 2, but most of these senesced without producing grain. Tiller 3 appeared on very few plants, but more emerged along with a few tiller 4's after heading in 1987.

For plants grown at 100 plants m^{-2}, most of the positive response of shoots $plant^{-1}$ to ethephon was confined to shoots which were present only in small numbers or not at all prior to the application of ethephon: tillers 4, 12, 21, and 30 in 1987 (Fig. 5.5); tillers 4, 21, and 30 in 1988 (Fig. 5.6); and tillers 4, 12, 21, 30, and 100 in 1989 (Fig. 5.7). While not significant, the contribution of tillers 11 and

Fig. 5.5. Shoots plant^{-1} contributed by specific shoots in the 1987 growing season for barley grown at 100 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.

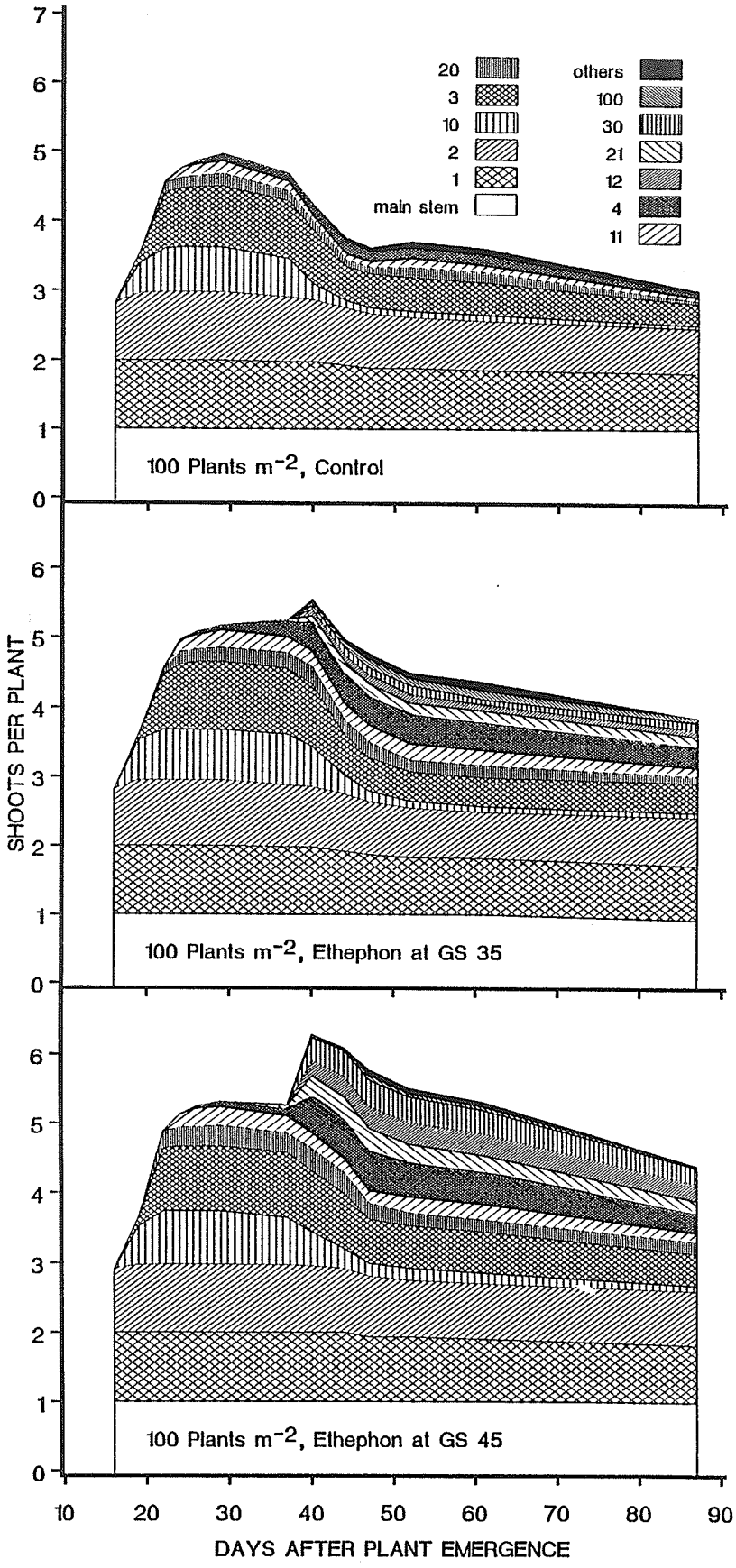

20
3
10
2
1
main stem
others
100
30
21
12
4
11
100 Plants m^{-2}, Control
100 Plants m^{-2}, Ethephon at GS 35
100 Plants m^{-2}, Ethephon at GS 45
SHOOTS PER PLANT
DAYS AFTER PLANT EMERGENCE
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90

Fig. 5.6. Shoots plant^{-1} contributed by specific shoots in the 1988 growing season for barley grown at 100 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.

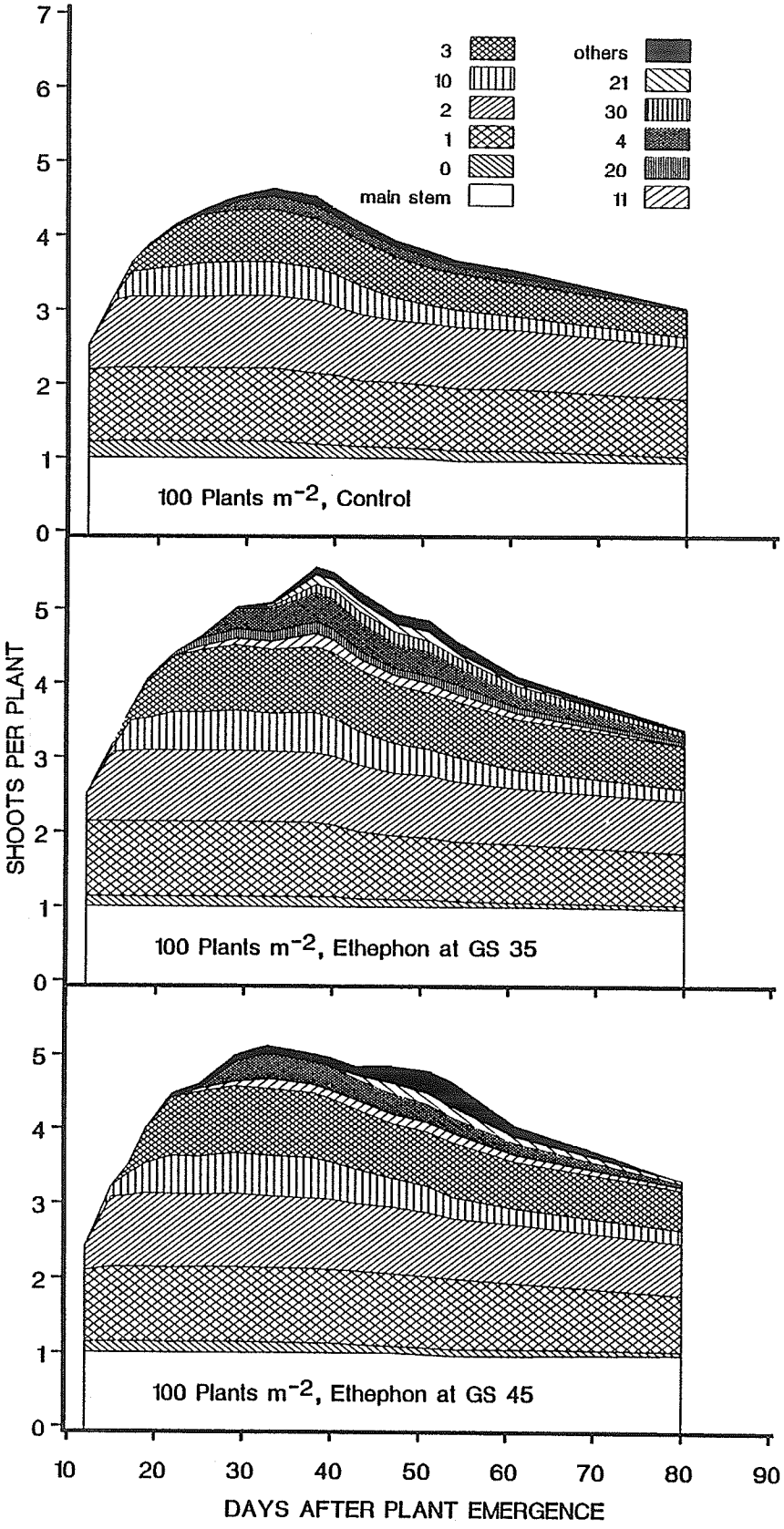
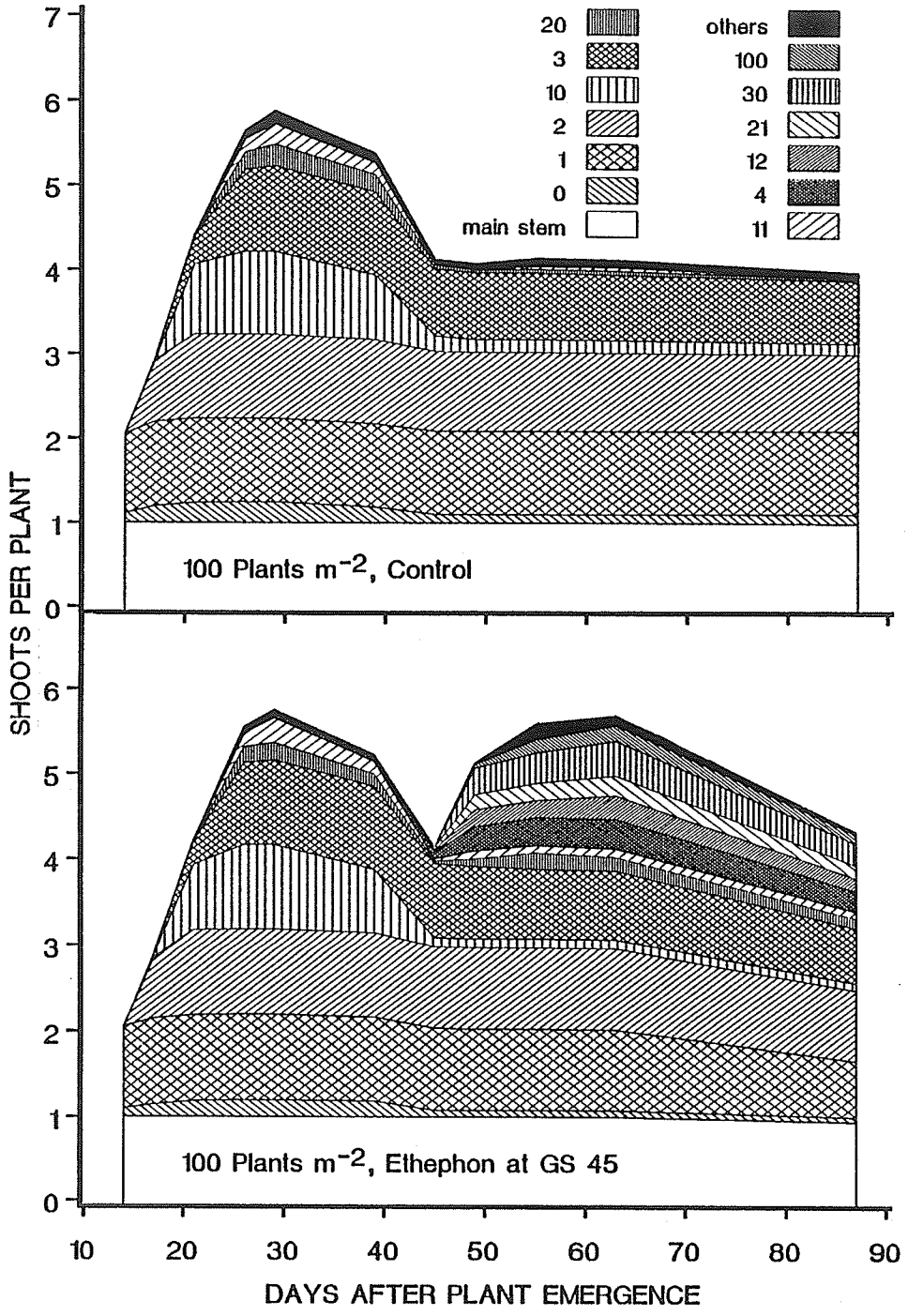

3
10
2
1
0
main stem
others
21
30
4
20
11
100 Plants m-2, Control
100 Plants m-2, Ethephon at GS 35
100 Plants m-2, Ethephon at GS 45
SHOOTS PER PLANT
DAYS AFTER PLANT EMERGENCE
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90

Fig. 5.7. Shoots plant^{-1} contributed by specific shoots in the 1989 growing season for barley grown at 100 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.


20
3
10
2
1
0
main stem
others
100
30
21
12
4
11
100 Plants m^{-2}, Control
100 Plants m^{-2}, Ethephon at GS 45
SHOOTS PER PLANT
DAYS AFTER PLANT EMERGENCE
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
90

20 in 1987 was enhanced by treatment with ethephon. Other shoots were not promoted by the application of ethephon. For plants grown at 300 plants m^{-2}, most of the positive response of shoots $plant^{-1}$ to ethephon was also confined to shoots which were present only in small numbers or not at all prior to the application of ethephon: tillers 3, 4, and 10 in 1987 (Fig. 5.8); tillers 3 and in 1988 (Fig. 5.9); and tillers 3, 4, 10, and 11 in 1989 (Fig. 5.10).

Plants were sampled and dissected at the time of ethephon application (GS 45) in 1988 and 1989 to give an indication of the numbers of tillers and tiller buds present per plant (Table 5.1). For purposes of this discussion, a tiller bud is defined as a bud which may be partially elongated, but which is enclosed in its prophyll and which has not yet emerged from its subtending leaf sheath. The buds present varied in length from less than 1 mm to over 100 mm; some of the longest buds extended for most of the length of their subtending leaf sheaths. A few buds were observed at locations other than those indicated, for example tiller buds 13, 22, and 5 on barley grown at 100 plants m^{-2}, and buds 11 and 20 on barley grown at 300 plants m^{-2}.

The survival of those shoots which appeared before ethephon was applied was not affected in 1987 or 1988 at either plant density, nor at the high plant density in 1989 (Table 5.2). However, for barley grown at 100 plants m^{-2} in 1989, the application of ethephon at GS 45 resulted in reduced survival for those shoots which appeared before it was applied. Reduced survival was most evident for tiller 1 (0.99 and 0.67 $plant^{-1}$ for control and ethephon treated plants, respectively); reduced survival was also evident for main stems of Samson (0.98 and 0.90 $plant^{-1}$ for control and ethephon treated plants, respectively, compared

Fig. 5.8. Shoots plant^{-1} contributed by specific shoots in the 1987 growing season for barley grown at 300 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.

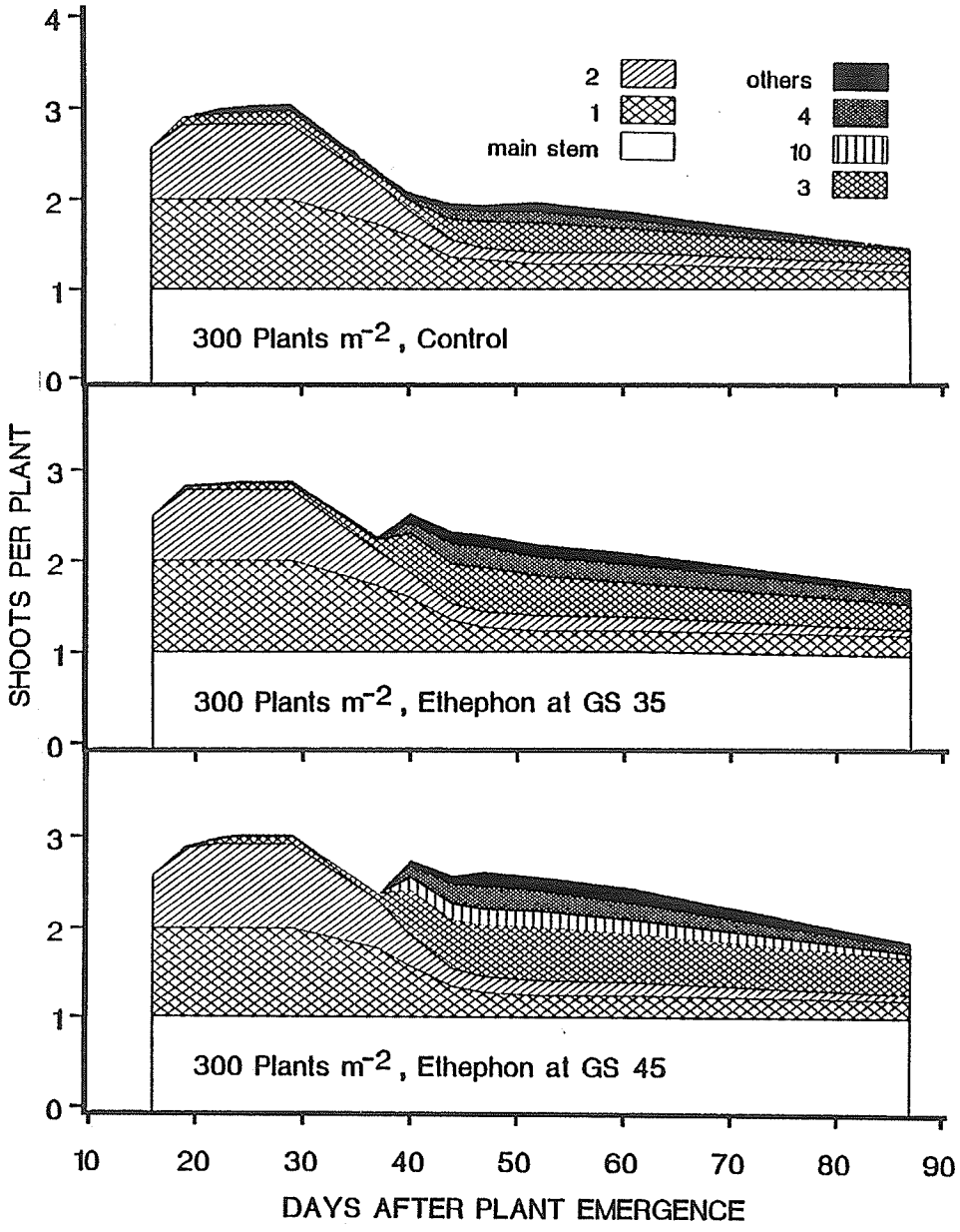

2
1
main stem
others
4
10
3
300 Plants m-2, Control
300 Plants m-2, Ethephon at GS 35
300 Plants m-2, Ethephon at GS 45
SHOOTS PER PLANT
0
1
2
3
4
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE

Fig. 5.9. Shoots plant^{-1} contributed by specific shoots in the 1988 growing season for barley grown at 300 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.

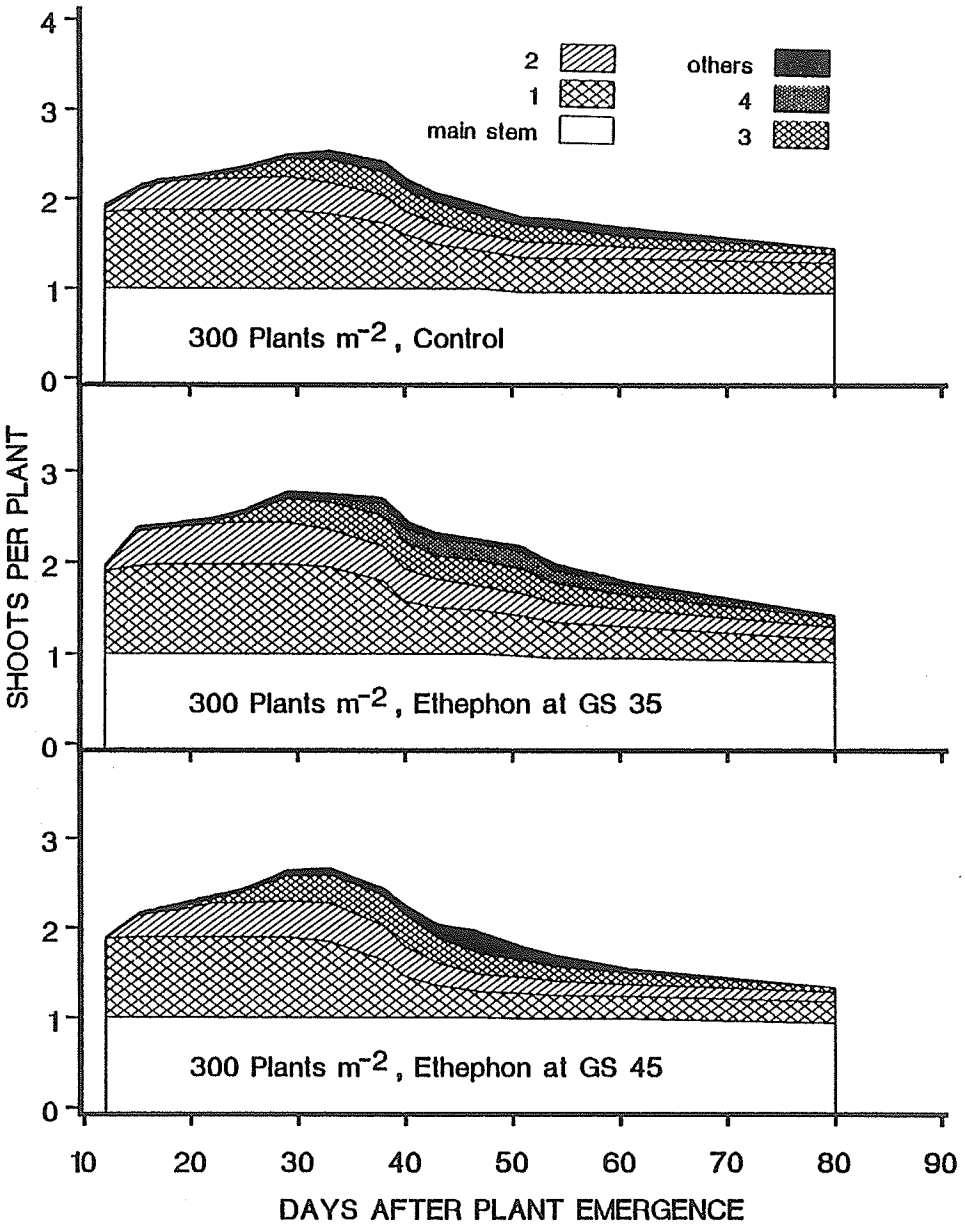

2
1
main stem
others
4
3
300 Plants m-2, Control
300 Plants m-2, Ethephon at GS 35
300 Plants m-2, Ethephon at GS 45
SHOOTS PER PLANT
0
1
2
3
4
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE

Fig. 5.10. Shoots plant^{-1} contributed by specific shoots in the 1989 growing season for barley grown at 300 plants m^{-2} with various ethephon treatments.

Note: The width in y-axis units of a pattern for a specific tiller indicates the contribution of that tiller to total shoots plant^{-1}.

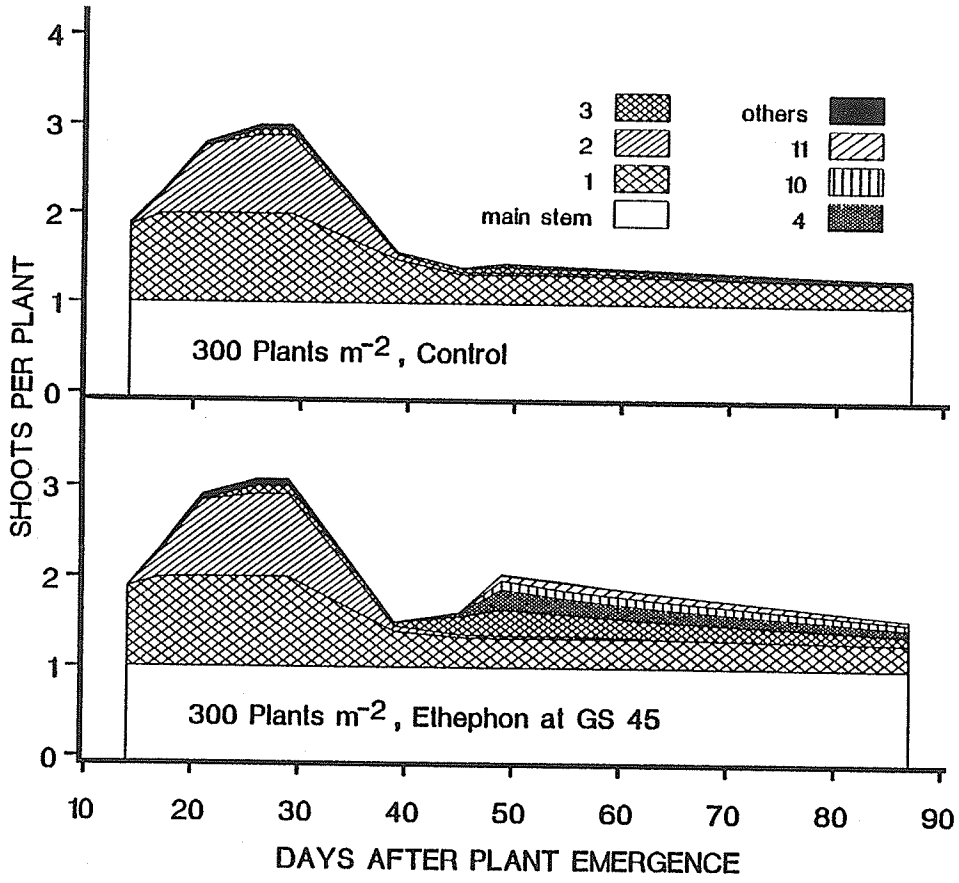

SHOOTS PER PLANT
4
3
2
1
0
3
2
1
main stem
others
11
10
4
300 Plants m^{-2}, Control
300 Plants m^{-2}, Ethephon at GS 45
10
20
30
40
50
60
70
80
90
DAYS AFTER PLANT EMERGENCE

Table 5.1. Status of tillers and tiller buds present at Zadoks GS 45 in 1988 and 1989, based on random sampling of 10 plants from each cultivar (Argyle and Samson).

Tiller or Bud Location	1988 Emerged Tillers	1988 Tiller Buds	1989 Emerged Tillers	1989 Tiller Buds
	(20 plants)$^{-1}$			
	100 Plants m^{-2}			
Main	20	0	20	0
0	0	0	1	0
1	19	0	19	0
10	2	15	11	2
11	0	19	4	9
12	0	17	0	15
100	0	0	0	5
2	19	0	17	0
20	0	15	5	10
21	0	19	0	14
3	12	8	19	0
30	0	10	0	12
4	1	14	0	16
Shoots or Buds Plant^{-1}	*3.7*	*5.9*	*4.8*	*4.2*
	300 Plants m^{-2}			
Main	20	0	20	0
1	9	1	5	0
10	0	9	0	3
2	7	9	0	2
3	8	12	0	17
4	2	12	0	9
Shoots or Buds Plant^{-1}	*2.3*	*2.4*	*1.3*	*1.6*

Table 5.2. Spikes plant^{-1} and grain yield plant^{-1} contributed by shoots appearing before or after ethephon application, for barley grown in the 1987, 1988, and 1989 seasons, at two plant densities, and with various ethephon treatments.

Ethephon Treatment	Spikes			Total Grain Yield		
	Before Θ	After	All	Before	After	All
	------ plant^{-1} ------			------ g plant^{-1} ------		
1987						
100 Plants m^{-2}						
Control	2.8 Ω	0.2 c	3.0 b	3.69 a	0.05 c	3.74
GS 35	3.0	0.8 b	3.9 a	3.45 ab	0.37 b	3.82
GS 45	3.2	1.2 a	4.4 a	3.12 b	0.54 a	3.67
300 Plants m^{-2}						
Control	1.3	0.2 b	1.5 b	1.70 a	0.06 b	1.76
GS 35	1.3	0.5 a	1.7 a	1.35 b	0.14 a	1.48
GS 45	1.3	0.6 a	1.9 a	1.35 b	0.17 a	1.52
1988						
100 Plants m^{-2}						
Control	3.0	0.0	3.0	3.24	0.01	3.26
GS 35	3.2	0.2	3.4	3.22	0.06	3.29
GS 45	3.3	0.1	3.3	3.06	0.01	3.07
300 Plants m^{-2}						
Control	1.5	0.0	1.5	1.46 a	0.00	1.46 a
GS 35	1.4	0.1	1.4	1.21 b	0.00	1.21 b
GS 45	1.3	0.0	1.3	1.30 b	0.00	1.30 b
1989						
100 Plants m^{-2}						
Control	3.9 a	0.0 b	3.9	6.29 a	0.00 b	6.29
GS 45	3.2 b	1.1 a	4.3	4.86 b	0.53 a	5.39
300 Plants m^{-2}						
Control	1.3	0.1 b	1.3	1.90	0.02	1.92
GS 45	1.3	0.3 a	1.5	1.80	0.06	1.86

Θ The terms "before", "after", and "all" with respect to shoot appearance refer to shoots which were first observed before ethephon application, after ethephon application, and all shoots present, respectively.

Ω Means within a column of treatments in a particular year and at a particular plant density are significantly different if followed by different letters, based on LSD(0.05).

with 1.0 and 0.98 plant^{-1} for control and ethephon treated Argyle plants, respectively). Although not significantly, tillers 2 and 3 showed reduced survival on treated plants compared with untreated plants.

Those shoots which appeared after ethephon application made substantial contributions to the spike populations for treated barley in 1987 and 1989 at both plant densities, but not in 1988 (Table 5.2). However, late appearing shoots in ethephon treated barley were only reflected in the total number of spikes in 1987, because the reduced number of early shoots in ethephon treated barley grown at 100 plants m^2 in 1989 partially negated the positive effect of ethephon on late appearing shoots.

Grain yield plant^{-1} was highest in 1989 and lowest in 1988. Yield plant^{-1} for barley grown at 100 plants m^{-2} was higher than for barley grown at 300 plants m^{-2}, but calculated on an area basis, plants at the higher density yielded more than those at the lower density in both 1987 and 1988. Grain yield contributed by shoots which appeared before ethephon application was reduced by ethephon in 1987 at both plant densities, in 1988 at 300 plants m^{-2}, and in 1989 at 100 plants m^{-2} (Table 5.2). Shoots which appeared after ethephon application made substantial contributions to grain yield in treated barley in 1987 and 1989; however, in no case did the increased yield contribution of late shoots more than compensate for the decreased yield contribution of early shoots.

5.4 Discussion.

Although in earlier studies (Bahry, 1988; Entz, 1988), Argyle and Samson had responded differently to the application of ethephon, in this study the two cultivars responded similarly in all three years (except as noted). Differential cultivar responses to ethephon have been reported (Bahry, 1988; Entz, 1988; Simmons et al., 1988; Dahnous et al., 1982), but the causes of such responses appear to be poorly understood.

Ethephon promoted the late appearance of shoots and their contribution to grain yield in 1987 and 1989, but much less in 1988. The reason for this year to year variation in the promotion of late appearing shoots by ethephon may be in the amount of moisture available to the crop through the growing season. Substantially more rain fell in June and/or July of 1987 and 1989 than in 1988 (Table 5.3). Results reported by Bahry (1988) and Simmons et al. (1988) suggest that the degree to which ethephon promotes late tillering may be influenced by moisture availability: in both studies, increased spikes area^{-1} due to ethephon application tended to coincide with seasons of higher rainfall. Studies in which ethephon would be applied to barley under controlled moisture conditions would be needed to confirm this suggestion.

Application of ethephon at GS 45 was more effective than at GS 35 in promoting the emergence and survival of late shoots in 1987. In contrast, application at GS 35 was more effective in promoting the emergence of late shoots in 1988, although few of these survived to contribute to grain yield. The different responses in each year of shoot numbers to ethephon applied at GS 35 or 45 may be attributable to the moisture conditions in each year - with 4 days separating the early and late applications of ethephon in 1988, it is possible that barley

Table 5.3. Rainfall for May, June, and July in the 1987, 1988, and 1989 growing seasons.

Month	Year		
	1987	1988	1989
	mm		
May	51.0	34.9	38.0
June	80.6	44.3	158.6
July	160.3	69.3	42.4

treated at GS 45 was under a greater degree of moisture stress than when treated at GS 35 (although moisture stress was at no time obvious), therefore ethephon had less effect in promoting the growth of late tillers.

As a general observation, the late tillers that appeared on barley treated with ethephon differed slightly from early tillers in morphology and early growth. Late tillers often emerged by splitting the sheath of the subtending leaf rather than emerging from between the leaf sheath and the stem at the leaf collar. Also, as earlier described by Aspinall (1961), the blade on the first leaf of late tillers tended to be very short and blunt, compared to the blade on the first leaf of early tillers.

It has been suggested that the increased spikes plant^{-1} associated with ethephon treatment of cereals was due to prevention of senescence of early tillers (Bahry, 1988; Hill et al., 1982). If ethephon did prevent senescence of early shoots, it might be expected that earlier application would be more effective than later application in increasing final shoot numbers, because tiller senescence is likely to be less advanced at GS 35 than at GS 45. In this study, ethephon did not prevent senescence of early shoots, instead either not affecting the survival of early shoots, or promoting senescence of early shoots as for barley grown at 100 plants m^{-2} in 1989. Lauer and Simmons (1989) recently reported that a decline in growth rate of non-surviving tillers was evident as early as 3-4 weeks after emergence. This suggests that by the time ethephon is applied at the boot stage, senescence processes are well under way for tillers which will senesce, and likely should not be expected to reverse due to the ethephon application.

Some of those tillers which senesced in response to ethephon did so with their heads in the boot, being quite advanced in development at the time when ethephon was applied. Failure of heads to emerge for cereal plants treated with ethephon has been reported, although such failure occurred at rates exceeding 2000 ppm, about eight times the rate used in this study (Hughes et al., 1974). Cox and Otis (1989) observed ethephon to enhance tiller senescence in winter wheat, and suggested that under the conditions of their study (400 g ha^{-1} applied at GS 39) ethephon seemed to promote processes leading to tiller senescence.

The observational data on the status of tillers and tiller buds at the time of ethephon application (Table 5.1) are not detailed enough to make conclusions as to critical stages for survival of emerged tillers or critical lengths or masses for promotion and survival of tiller buds. However, the data do suggest that those late tillers which survived and contributed to grain yield were likely present as partially elongated tiller buds at the time when ethephon was applied. Emerged tillers 1, 10, 2, 20, 3 at 100 plants m^{-2}, and 1 and 2 at 300 plants m^{-2} were or had been present on all plants at the time of ethephon application; therefore, their numbers were not promoted. Non-emerged but partially elongated tiller buds were present in the axils of leaves 4, 12, 21, and 30 at 100 plants m^{-2}, and 3, 4 and 10 at 300 plants m^{-2} on most plants at the time of ethephon application; therefore, these were the tillers that were promoted by ethephon. The smaller increase in shoots $plant^{-1}$ for barley grown at 300 plants m^{-2} can be explained by the smaller number of partially elongated tiller buds present on plants at the high plant density - because plants grown at the high density produced fewer

tillers in the first place, there were fewer potential sites on the plant for additional tiller buds to develop.

The restricted growth of such buds during elongation of adjacent stems has been attributed to the demand of the rapidly developing stem and inflorescence for photosynthate at the expense of the tiller buds (Johnston and Jeffcoat, 1977). The outgrowth of these buds in response to ethephon application may be due to reduced auxin transport to bud sites caused by ethylene released from ethephon; restricted transport of auxin to axillary buds by ethylene, and subsequent bud outgrowth has been demonstrated for oat (Harrison and Kaufman, 1984) and *Phaseolus vulgaris* (Hillman and Yeang, 1979). Woodward and Marshall (1988) reported that tiller emergence during the normal tillering phase of barley was promoted by ethephon, and attributed the effect to interference with auxin transport. These results may explain late tiller growth in response to ethephon application. However, other changes in barley growth sometimes caused by ethephon (restricted stem elongation, reduced kernel number and kernel weight) suggest that changes in the partitioning of photosynthate between various parts of the plant may also be involved in the observed growth of tiller buds after ethephon application (this possibility is the subject of a study reported in a later chapter).

Under the growth conditions of this study, ethephon had either no effect or a negative effect on grain yield per plant. In 1987 and 1989, late shoots on plants treated with ethephon contributed as much as 15% of grain yield per plant; however, because of the reduced yield contribution of early shoots, the net effect of ethephon on grain yield was nil or negative. The reduced yield contribution of early shoots in

all three years was attributable to reductions in the number of kernels per shoot and in kernel weight on plants treated with ethephon (chapter six).

Aside from its effect of increasing lodging resistance, the effect of ethephon in promoting the appearance of late shoots has a positive influence on grain yield. Compensation for the negative effects of ethephon on kernel number depends on the promotion of late tillers and their survival to maturity. Given that the production and survival of late shoots seems greatly dependent on environmental conditions, particularly moisture, the risk inherent in the use of ethephon under Canadian Prairie conditions is that in relatively dry years, or perhaps even in years with an unfavorable seasonal rainfall distribution, late shoots will fail to compensate for the reduced kernel numbers on early shoots with a net negative effect on grain yield. Because of this risk, the use of ethephon by growers in western Canada must be determined by a management decision based on knowledge of current environmental conditions and the likelihood of severe lodging.

6. KERNELS SPIKE^{-1} AND KERNEL WEIGHT IN BARLEY TREATED WITH ETHEPHON.

6.1 Abstract.

Treatment of barley with ethephon may reduce lodging and increase kernel weight, but reductions in kernel weight and kernels spike^{-1} are also often observed. This study examined the effect of ethephon on kernels spike^{-1} and average kernel weight for spikes on specific shoots which appeared before or after ethephon application. Argyle and Samson barley were grown at 100 and 300 plants m^{-2} and treated with ethephon at Zadoks GS 35 and/or 45 in 1987, 1988, and 1989. Kernels spike^{-1} and average kernel weight were determined for each spike produced on 10 plants plot^{-1} for which the date of emergence of each tiller had been recorded. The cultivars did not differ significantly in their response to ethephon. Kernels spike^{-1} was consistently reduced by ethephon application, which was attributed to both the promotion of late-appearing shoots with relatively few kernels, and the abortion of florets on main stems and early appearing tillers due to ethephon's gametocidal properties. Kernel weight was reduced, not affected, and increased by ethephon in 1987, 1988, and 1989, respectively. Differences in competition between developing kernels and late tillers, in lodging, and in nitrogen availability may account for the variable kernel weight responses observed. Kernels spike^{-1} and/or kernel weight reductions generally resulted in decreased yield plant^{-1} for barley grown at 300 plants m^{-2}, but such reductions were at least partially compensated by increased spikes plant^{-1} for barley grown at 100 plants m^{-2} in 1987 and 1989. The risk of negative responses to ethephon makes the use of ethephon in Western Canada advisable only when the risk of severe lodging is known to be high.

6.2 Introduction.

Ethephon effectively reduces lodging in treated barley. However, irrespective of its effect on plant height and lodging, ethephon often affects yield components and yield. Spikes $area^{-1}$ has been increased or unaffected by ethephon application (Bahry, 1988; Simmons et al., 1988), while kernels $spike^{-1}$ was decreased or unaffected (Bahry, 1988; Simmons et al., 1988). Kernel weight has been reported to increase (Simmons et al., 1988), decrease, or be unaffected (Bahry, 1988; Simmons et al., 1988) by ethephon application.

The reductions in kernels $spike^{-1}$ observed may be related to previously reported gametocidal properties of ethephon (Hughes, 1975; Stoskopf and Law, 1972). While evaluating the potential of ethephon as a male sterilant for use in hybrid cereal breeding programs, Stoskopf and Law (1972) observed three types of gametocidal responses in barley treated with ethephon: the sterilization of all three anthers per floret with no pollen produced, the sterilization of one or two anthers and pollen release in the remaining anther retarded about seven days, and pollen release in all three anthers retarded about seven days. Ethephon appears to act as a gametocide through a general disruption of processes in developing anthers (Colhoun and Steer, 1983). The initiation of meiosis in pollen mother cells appears to be a critical stage, after which ethephon has minimal influence on pollen development (Hughes, 1975).

Increases in kernel weight have been observed when treatment with ethephon has prevented lodging in barley (Foy and Witt, 1987; Hill et al., 1982; Simmons et al., 1988). The reasons for decreases in kernel weight caused by ethephon application are not known.

The objective of this study was to investigate the effects of ethephon on kernels spike^{-1} and average kernel weight for specific spikes and for spikes grouped according to whether the shoots on which they appeared emerged before or after ethephon application to barley.

6.3 Materials and Methods.

Details of cultural practices and experimental design are given in chapter three. Kernels spike^{-1} and average kernel weight (grain yield spike^{-1} divided by kernels spike^{-1}) were determined for each spike from the 10 plants plot^{-1} for which tiller emergence and senescence was observed over each growing season; therefore, kernels spike^{-1} and kernel weight could be determined for specific spikes and for spikes grouped according to whether the shoots on which they appeared emerged before or after ethephon application (details of tiller and spike characterization are given in chapter five).

In 1988 and 1989, 10 main stem heads were sampled from ethephon treated and untreated plots of each cultivar at 300 plants m^{-2}. Florets which aborted prior to fertilization and developing kernels at each rachis node were counted and the numbers recorded.

Analysis of variance was performed for each data set. Unless otherwise noted, differences with $P<0.05$ were considered meaningful.

6.4 Results.

Argyle and Samson barley rarely differed in kernels spike^{-1}, kernel weight, or yield plant^{-1}. Unless otherwise noted, no cultivar by ethephon treatment interactions were evident for kernels spike^{-1}, kernel weight, or yield plant^{-1}.

For barley grown at 100 plants m^{-2}, kernels spike^{-1} was highest in 1989, and lowest in 1988 (Table 6.1). In barley not treated with ethephon, kernels spike^{-1} declined for successive tillers, and was lowest for late appearing shoots (after GS 35 or 45). Overall kernels spike^{-1} was reduced by ethephon application in all three years, as was kernels spike^{-1} for those shoots which appeared before GS 35 or 45, while for shoots appearing after this time, ethephon apparently increased kernels spike^{-1}. Due to the relatively low frequency of appearance of any one specific late-appearing shoot among the 10 plants plot^{-1} under observation, variability for kernels spike^{-1} for specific late appearing shoots was high (CV > 50%); therefore, data for late-appearing shoots are given collectively and not on the basis of individual shoots. For spikes formed on the shoots present in the majority at GS 35 or 45 (main stems, T1, T2, and T3), reductions in kernels spike^{-1} caused by ethephon were evident, except for T3 in 1987 and 1988, when kernels spike^{-1} was increased and not affected, respectively.

Application of ethephon at GS 45 generally caused a larger reduction in kernels spike^{-1} than application at GS 35 (Table 6.1). For main stems, the reduction was similar for both ethephon application times in 1987 and 1988, while for tillers 1, 2, and 3, application at GS

Table 6.1. Kernels spike^{-1} and kernels plant^{-1} of specific spikes or groupings of spikes for barley grown at 100 plants m^{-2} with various ethephon treatments.

Ethephon	SpikeΘ				Spike GroupΩ		
Treatment	MS	T1	T2	T3	Before	After	All
	kernels spike$^{-1}\Delta$						
1987							
Control	55.0 aΨ	46.4 a	44.1 ab	26.5 b	48.3 a	14.0 b	46.5 a
GS 35	45.8 b	44.8 a	47.9 a	45.4 a	46.2 a	28.8 a	41.7 b
GS 45	45.6 b	35.4 b	39.3 b	37.7 ab	41.4 b	31.0 a	38.3 b
1988							
Control	50.0 a	40.7 Φ	39.1 a	32.8	41.5 a	5.5	41.4 a
GS 35	42.6 b	37.5	38.3 a	34.5	37.9 b	11.5	37.1 b
GS 45	43.1 b	36.4	30.9 b	31.5	35.6 b	2.3	35.0 b
1989							
Control	54.7 a	50.1 a	50.5 a	47.8 a	50.6 a	1.1 b	50.2 a
GS 45	47.8 b	40.0 b	39.8 b	37.2 b	42.2 b	22.3 a	37.2 b
	kernels plant^{-1}						
1987							
Control	55.0 a	38.1	29.0	11.7	136.0	3.1 c	139.1Φ
GS 35	42.8 b	35.6	33.9	19.5	138.3	22.1 b	160.4
GS 45	44.9 b	29.2	31.0	16.9	131.5	34.9 a	166.4
1988							
Control	46.9 a	32.4	28.2	11.8	125.2	0.6	125.7
GS 35	41.5 b	26.4	26.9	20.1	122.7	3.0	125.7
GS 45	42.1 b	27.2	22.1	17.1	115.9	0.4	116.3
1989							
Control	54.0 a	49.5 a	46.8 a	36.4 a	198.9 a	0.2 b	199.1 a
GS 45	45.0 b	26.7 b	31.9 b	24.1 b	135.2 b	24.9 a	160.2 b

Θ Means given for main stems (MS), and tillers 1, 2, and 3 (T1, T2, and T3, respectively), the shoots present in greatest numbers both at ethephon application and at harvest.

Ω The terms "before", "after", and "all" refer to spikes grouped according to when the shoots on which they appeared were first observed: before ethephon application, after ethephon application, and all spikes present, respectively.

Δ Kernels spike^{-1} is per spike present; kernels plant^{-1} is equivalent to the product of kernels spike^{-1} and spikes plant^{-1}.

Ψ Means within a column of ethephon treatments for a particular year are significantly different if followed by different letters, based on LSD(0.05).

Φ Overall ethephon treatment F-test NS; orthogonal contrast of control vs. ethephon (mean of two ethephon treatments) significant at $P<0.05$.

35 caused either no reduction or a reduction comparable to that caused by application at GS 45.

Barley grown at 300 plants m^{-2} behaved similarly to that grown at the lower density in that overall kernels $spike^{-1}$ was highest in 1989 and 1987, lowest in 1988, and tended to be reduced by ethephon (Table 6.2). In 1988, ethephon treatment at GS 35 appeared to cause a greater reduction in kernels $spike^{-1}$ overall, for main stems, and for shoots present at the time of application than treatment at GS 45. In these cases, cultivar by ethephon treatment interactions were significant at $P<0.05$, and the greater reduction caused by the early ethephon application was restricted to Argyle barley.

Main stem inflorescences of plants grown at 300 plants m^{-2} produced florets at 20.5 ($\pm$1.7) and 20.3 ($\pm$1.8) rachis nodes in 1988 and 1989, respectively, and ethephon treatment did not affect the number of nodes at which florets were produced. Main stem spikes sampled at approximately mid-grain filling from barley grown at 300 plants m^{-2} had 48.6 and 43.2 developing kernels for control and ethephon treated plants in 1988, and 49.6 and 44.8 developing kernels for control and ethephon treated plants in 1989, respectively (differences significant based on LSD(0.05)). For untreated plants, many florets at the basal 4-5 rachis nodes aborted prior to fertilization, with sporadic abortion evident along the rest of the rachis and slightly concentrated at the apical end (Fig.'s 6.1-6.2). Additional floret abortion was evident for ethephon treated plants compared with untreated plants, concentrated at the apical end of the rachis, but also at rachis nodes 5-7 and sporadically along the remainder of the rachis.

Table 6.2. Kernels spike^{-1} and kernels plant^{-1} of main stems or groupings of spikes for barley grown at 300 plants m^{-2} with various ethephon treatments.

Ethephon Treatment	Main StemΘ	Spike GroupΩ		
		Before	After	All
	kernels spike^{-1}Δ			
1987				
Control	49.2 aΨ	47.6 a	10.5 Φ	43.9 a
GS 35	40.9 b	40.0 b	18.8	34.6 b
GS 45	42.4 b	39.9 b	21.5	33.2 b
1988				
Control	42.0 a	36.9 a	0.0	36.9 a
GS 35	35.2 c	32.7 b	1.6	31.7 b
GS 45	38.5 b	35.2 a	0.0	35.2 a
1989				
Control	47.6	45.0	7.8	44.1 a
GS 45	45.5	43.2	10.9	38.4 b
	kernels plant^{-1}			
1987				
Control	49.2 a	60.2 a	3.3 a	63.5
GS 35	38.9 b	50.4 b	8.6 b	58.9
GS 45	42.4 b	50.4 b	11.4 b	61.9
1988				
Control	40.0 a	54.1 a	0.0	54.1 a
GS 35	32.2 b	44.8 b	0.3	45.1 b
GS 45	36.2 ab	46.8 b	0.0	46.8 b
1989				
Control	47.0	57.7	0.8	58.6
GS 45	45.0	55.1	3.4	58.5

Θ Means given for main stems (MS), the shoots present in greatest numbers both at ethephon application and at harvest.
Ω The terms "before", "after", and "all" refer to spikes grouped according to when the shoots on which they appeared were first observed: before ethephon application, after ethephon application, and all spikes present, respectively.
Δ Kernels spike^{-1} is per spike present; kernels plant^{-1} is equivalent to the product of kernels spike^{-1} and spikes plant^{-1}.
Ψ Means within a column of ethephon treatments for a particular year are significantly different if followed by different letters, based on LSD(0.05).
Φ Overall ethephon treatment F-test NS; orthogonal contrast of control vs. ethephon (mean of two ethephon treatments) significant at $P<0.05$.

Fig. 6.1. Fertilized and aborted florets spike^{-1} for main stem inflorescences approximately 3 weeks after ethephon application to barley grown at 300 plants m^{-2} in 1988:

a. Control

b. Ethephon at GS 45.

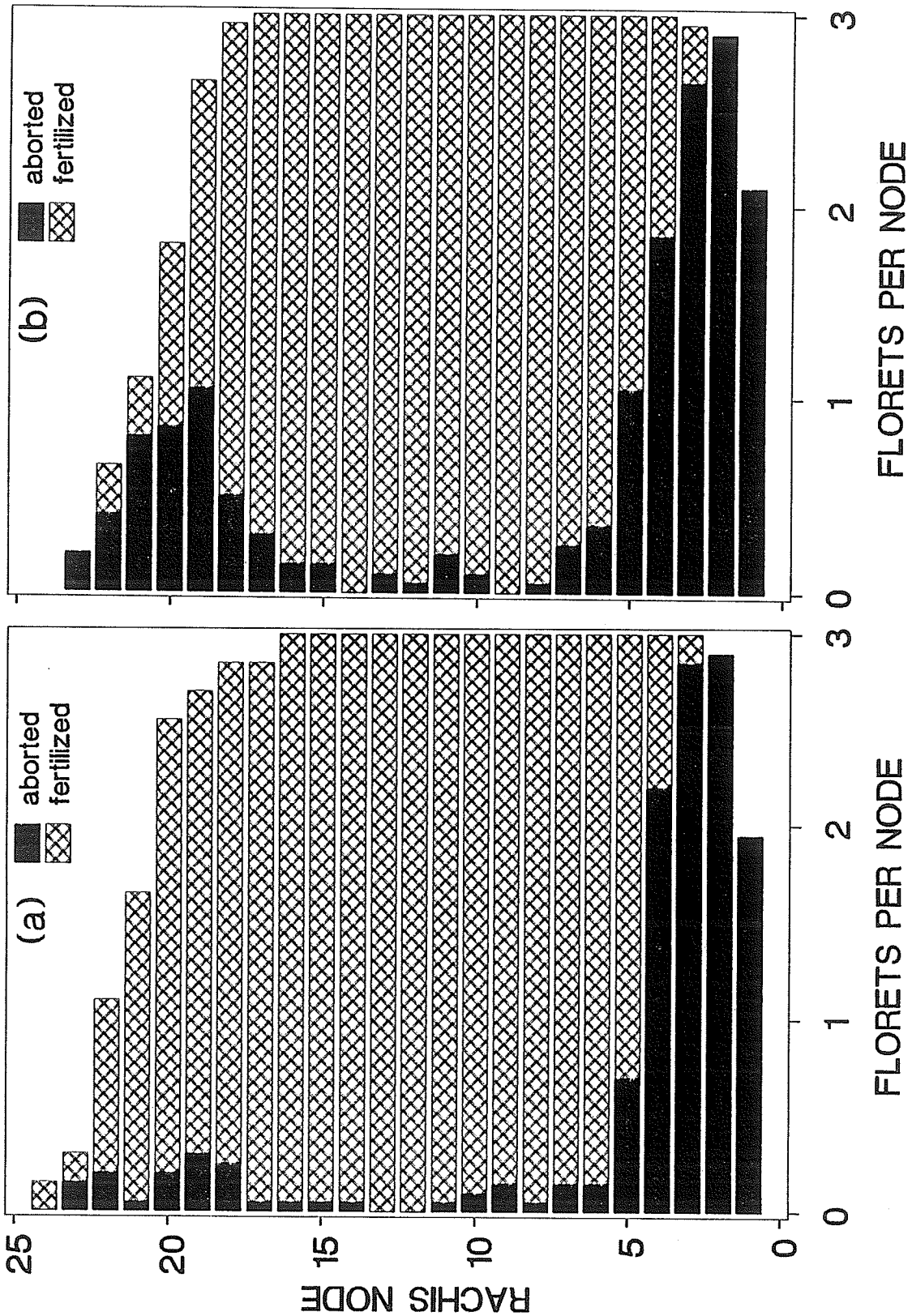
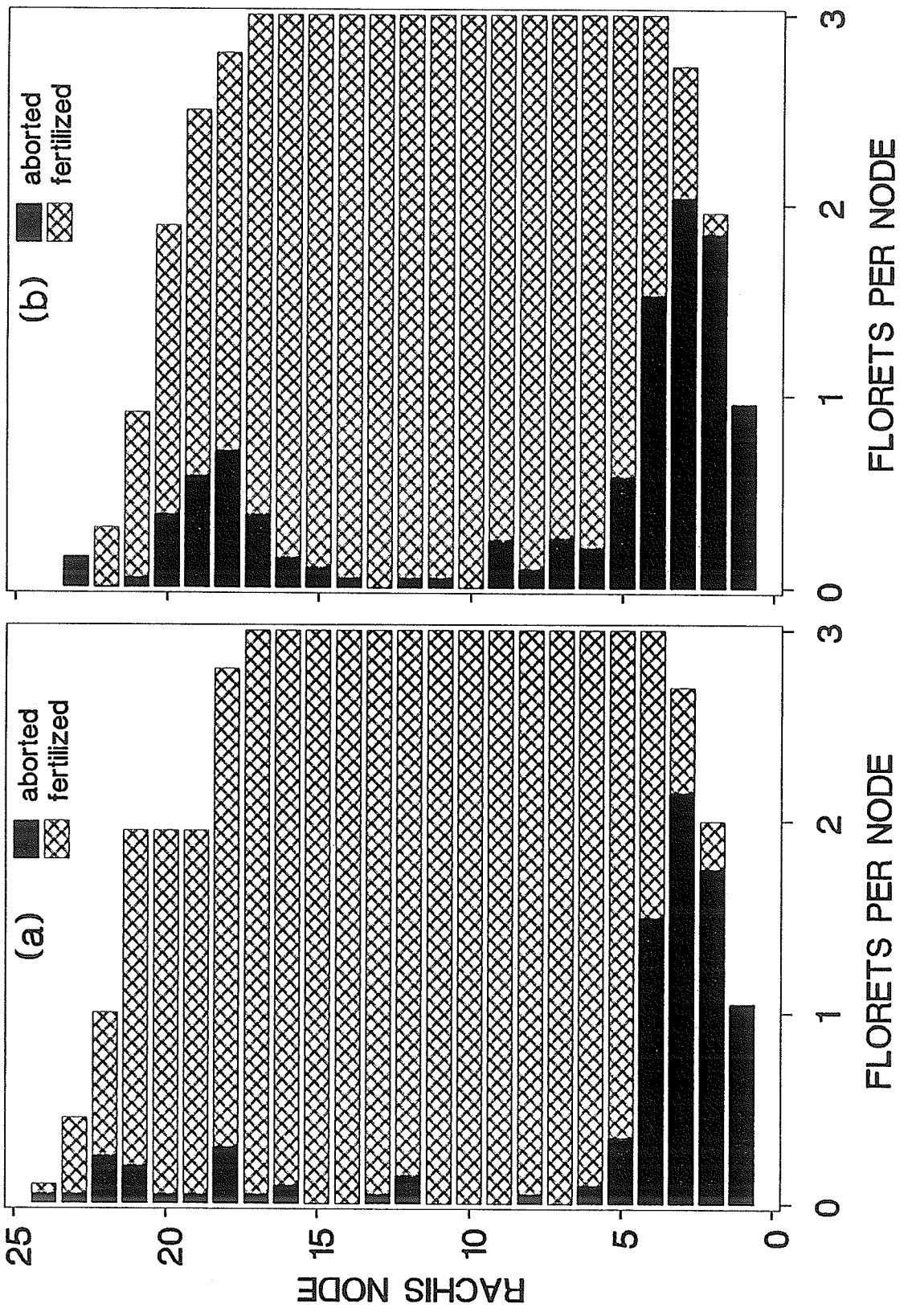

(a)
aborted
fertilized
(b)
aborted
fertilized
RACHIS NODE
25
20
15
10
5
0
0
1
2
3
FLORETS PER NODE
FLORETS PER NODE

Fig. 6.2. Fertilized and aborted florets spike^{-1} for main stem inflorescences approximately 3 weeks after ethephon application to barley grown at 300 plants m^{-2} in 1989:

a. Control

b. Ethephon at GS 45.


(a)
aborted
fertilized
(b)
aborted
fertilized
RACHIS NODE
25
20
15
10
5
0
0
1
2
3
FLORETS PER NODE
FLORETS PER NODE

Contributions of individual shoots to kernels plant^{-1} were reduced (MS) or tended to be reduced (T1 and T2) by ethephon application to barley grown at 100 plants m^{-2} in 1987 and 1988 (Table 6.1). In 1987 and 1988, the contribution to kernels plant^{-1} of shoots which appeared before GS 35 or 45 was not affected by ethephon. Because of the contribution of tillers appearing after ethephon application, total kernels plant^{-1} was increased in 1987. In 1989, ethephon reduced the contribution to kernels plant^{-1} for MS, T1, T2, and T3. Although late shoots contributed more kernels plant^{-1} in ethephon treated plants than in untreated plants, the contribution did not compensate for the reduced contribution of shoots which first appeared before GS 35 or 45; therefore, total kernels plant^{-1} was reduced by ethephon application.

For barley grown at 300 plants m^{-2}, contributions of main stems and all shoots appearing before GS 35 or 45 to kernels plant^{-1} were reduced by ethephon in 1987 and 1988 (Table 6.2). Late appearing shoots made a significant contribution to kernels plant^{-1} in ethephon treated barley in 1987, so there was no net effect of ethephon on total kernels plant^{-1}, while in 1988, total kernels plant^{-1} was reduced by ethephon. Kernels plant^{-1} for barley grown at the high density was not affected by ethephon in 1989.

Kernel weights for barley grown at 100 plants m^{-2} were highest in 1989, followed by 1987, then 1988 (Table 6.3). As with kernels spike^{-1}, kernel weights declined for successive tillers, and were lowest for late appearing shoots (after GS 35 or 45). In 1987, ethephon application reduced average kernel weights based on all spikes and on spikes produced on shoots which appeared before ethephon was applied; the same tendency was evident for main stems, T1, and T2. Ethephon application

Table 6.3. Kernel weight, and grain yield plant^{-1} of specific spikes or groupings of spikes for barley grown at 100 plants m^{-2} with various ethephon treatments.

Ethephon	SpikeΘ				Spike GroupΩ		
Treatment	MS	T1	T2	T3	Before	After	All
	mg kernel^{-1}						
1987							
Control	28.5 Ψ	26.7	26.2	18.6	27.4 a	14.7	27.1 a
GS 35	26.7	25.5	25.2	22.9	25.2 ab	17.2	24.1 b
GS 45	26.6	25.3	24.3	18.4	24.4 b	15.9	22.6 b
1988							
Control	27.9	26.8	23.9	21.5	25.8	4.7	25.8
GS 35	29.6	26.6	25.3	23.0	26.4	12.9	26.3
GS 45	29.1	26.6	25.9	24.3	26.5	10.0	26.5
1989							
Control	32.8 b	32.2 b	32.3	30.7 b	32.1 b	0.0 b	32.1
GS 45	34.7 a	33.6 a	39.9	34.5 a	35.8 a	21.1 a	33.6
	g plant^{-1}						
1987							
Control	1.57 a	1.01 a	0.77	0.30	3.69	0.05 c	3.74
GS 35	1.13 b	0.90 ab	0.85	0.44	3.45	0.37 b	3.82
GS 45	1.18 b	0.71 b	0.74	0.33	3.12	0.54 a	3.67
1988							
Control	1.33	0.87	0.68	0.25 Φ	3.24	0.01	3.26
GS 35	1.22	0.70	0.67	0.47	3.22	0.06	3.29
GS 45	1.22	0.72	0.57	0.40	3.06	0.01	3.07
1989							
Control	1.74 a	1.58 a	1.49	1.09	6.29 a	0.00 b	6.29
GS 45	1.56 b	0.89 b	1.32	0.83	4.86 b	0.53 a	5.39

Θ Means given for main stems (MS), and tillers 1, 2, and 3 (T1, T2, and T3, respectively), the shoots present in greatest numbers both at ethephon application and at harvest.

Ω The terms "before", "after", and "all" refer to spikes grouped according to when the shoots on which they appeared were first observed: before ethephon application, after ethephon application, and all spikes present, respectively.

Ψ Means within a column of ethephon treatments for a particular year are significantly different if followed by different letters, based on LSD(0.05).

Φ Overall ethephon treatment F-test NS; orthogonal contrast of control vs. ethephon (mean of two ethephon treatments) significant at $P<0.05$.

at GS 35 did not cause as great a reduction in kernel weight as application at GS 45. In contrast, ethephon tended to increase kernel weights in 1988, although none of the increases was significant at $P<0.05$; ethephon increased kernel weights in 1989, although for all spikes together, the increase was not significant. Application at GS 35 in 1988 was similar to application at GS 45 in its effect on kernel weight.

For barley grown at 300 plants m^{-2} in 1987, kernel weights tended to be reduced by ethephon, except for spikes appearing after ethephon application (Table 6.4). Although overall ethephon treatment differences were not significant, the orthogonal contrast control vs. ethephon (application times combined) was significant for kernel weights of spikes on late appearing shoots and of all spikes together. Kernel weights were not affected by ethephon in 1988. Except for spikes on late appearing shoots, kernel weights in 1989 tended to be reduced by ethephon and the reduction for all shoots taken together was significant at $P<0.10$.

For barley grown at 100 plants m^{-2}, overall grain yield $plant^{-1}$ and grain yield contributed by shoots which were present at GS 35 or 45 tended to be reduced by ethephon application, while in 1987 and 1989, late appearing shoots made substantial contributions to grain yield in ethephon treated barley (chapter five, Table 6.3). The contributions to yield $plant^{-1}$ made by main stems and T1's were reduced by ethephon in 1987 and 1989, and a tendency toward reduction was evident for main stems and T1's in 1988, and T2 and T3 in 1989 (Table 6.3).

Grain yield $plant^{-1}$ and grain yield contributed by shoots which were present at GS 35 or 45 was reduced by ethephon application in 1987

Table 6.4. Kernel weight and grain yield plant^{-1} of main stems or groupings of spikes for barley grown at 300 plants m^{-2} with various ethephon treatments.

Ethephon Treatment	Main StemΘ	Spike GroupΩ		
		Before	After	All
	mg kernel^{-1}			
1987				
Control	29.4 Ψ	28.6	9.7 Φ	27.9 Φ
GS 35	27.7	27.0	16.2	25.3
GS 45	27.8	26.9	15.0	24.8
1988				
Control	27.9	26.9	0.0	27.0
GS 35	28.7	26.8	2.0	26.8
GS 45	28.8	27.6	0.0	27.8
1989				
Control	34.1	33.8	6.8	33.6
GS 45	33.1	32.7	11.5	31.9
	yield plant^{-1}			
1987				
Control	1.44 a	1.70 a	0.06 b	1.76 Φ
GS 35	1.07 b	1.35 b	0.14 a	1.48
GS 45	1.18 b	1.35 b	0.17 a	1.52
1988				
Control	1.12 a	1.45 a	0.00	1.46 a
GS 35	0.91 b	1.20 b	0.00	1.21 b
GS 45	1.04 ab	1.29 b	0.00	1.30 b
1989				
Control	1.58	1.90	0.02	1.92
GS 45	1.49	1.80	0.06	1.86

Θ Means given for main stems (MS), the shoots present in greatest numbers both at ethephon application and at harvest.
Ω The terms "before", "after", and "all" refer to spikes grouped according to when the shoots on which they appeared were first observed: before ethephon application, after ethephon application, and all spikes present, respectively.
Ψ Means within a column of ethephon treatments for a particular year are significantly different if followed by different letters, based on LSD(0.05).
Φ Overall ethephon treatment F-test NS; orthogonal contrast of control vs. ethephon (mean of two ethephon treatments) significant at $P<0.05$.

and 1988 for barley grown at 300 plants m^{-2}, and late appearing shoots made a significant contribution to grain yield in ethephon treated barley only in 1987 (chapter five, Table 6.4). Main stems were virtually the only shoots present at ethephon application, and main stem yield contributions were reduced by ethephon application in 1987 and 1988 (Table 6.4). In 1988, ethephon applied at GS 35 appeared to reduce main stem grain yield more than ethephon applied at GS 45; in this case, the cultivar by ethephon treatment interaction was significant at $P<0.05$, and the greater reduction of yield when ethephon was applied at GS 35 compared with application at GS 45 was limited to Argyle barley.

6.5 Discussion.

The observation of tiller emergence, tiller senescence, and contribution to yield of specific tillers in plants treated with ethephon indicated that ethephon promoted the emergence of tillers relatively late in crop development, after heading, but also that such late appearing tillers could make a substantial contribution to grain yield (chapter five). The yield component observations made for individual shoots allow for the more detailed examination of ethephon effects on kernels spike^{-1} and kernel weight presented here compared with the observation of kernels spike^{-1} and kernel weight based on bulk harvested samples.

Ethephon applied to barley caused reductions in kernels spike^{-1} in all three years of the study, for both plant densities. This is consistent with the observations of others (Bahry, 1988; Simmons et al., 1988). The potential of ethephon to induce male sterility in cereal florets (Hughes et al., 1975; Stoskopf and Law, 1972) provides part of the explanation for the observed reductions in kernels spike^{-1}, especially in cases where actual reductions were observed for specific shoots (main stems, T1, T2, T3). However, in two of the three years of this study, a further apparent reduction in kernels spike^{-1} was attributable to the promotion of tiller emergence caused by ethephon (chapter five). Fewer kernels were produced on tillers emerging after ethephon application compared with those which emerged before ethephon application; therefore, in 1987 and 1989, kernels spike^{-1} for ethephon treated barley was apparently reduced compared with untreated barley partly because the former included many late tillers while the latter did not. The apparent increase of kernels spike^{-1} with ethephon

application for late appearing shoots compared with untreated barley was due to the increased frequency of appearance and promoted growth of such tillers rather than to a direct increase of kernels spike^{-1}.

The reduced kernels spike^{-1} found on main stems and early tillers implies that lodging resistance in ethephon treated barley is in part conferred by the reduced weight often carried on stems, since any factor which decreases the force applied to a cereal stem will decrease the tendency to lodge (Neenan and Spencer-Smith, 1975). Lodging resistance in ethephon treated barley has been attributed to reduced stem elongation (Brown and Early, 1973; Entz, 1988; Neenan and Spencer-Smith, 1975), and possibly enhanced stem strength (Selga et al., 1985).

Kernels spike^{-1} for main stems of barley grown at the low plant density was reduced similarly by application of ethephon at GS 35 or 45 in 1987 and 1988, while kernels spike^{-1} for T2 was not affected by application at GS 35. For T1, kernels spike^{-1} was not affected by application at GS 35 in 1987, but was reduced in 1988. This variable response may be explained by the gametocidal properties of ethephon: apparently, similar numbers of main stem florets were near the critical pre-meiotic pollen mother cell stage at either GS 35 or 45, while for T2, no florets were at a critical stage when ethephon was applied at GS 35, and for T1, some florets were at a critical stage in 1988 but not 1987. Generally, barley was somewhat more sensitive to reductions in kernels spike^{-1} when ethephon was applied at GS 45 than at GS 35; however, early boot stage (GS 41-45) applications are most effective for lodging control (Brown and Early, 1973).

The observation that floret abortion in ethephon treated spikes tended to be concentrated in the basal and apical regions of the spike

provides further evidence that ethephon induced reductions in kernels spike^{-1} can be attributed to ethephon's gametocidal properties. Floret maturity is known to be less advanced at a given time in the basal and apical region of the spike compared with the central region (Bonnett, 1935), providing for the possibility that when ethephon is applied, some florets may be before or beyond the most sensitive stage of development. Stoskopf and Law (1972) observed complete sterilization of all three anthers in some florets on ethephon treated plants, but some anthers in other florets were merely delayed in pollen release. Although sequential microscopic examinations would be necessary for confirmation, such a delay in pollen release may contribute to the general delay in maturity observed with ethephon application (chapter four), even though late tillers probably make a greater contribution to the maturity delay.

Ethylene release from ethephon is known to be temperature dependent, increasing in rate with temperature (Olien and Bukovac, 1978), offering a potential explanation for the differences in magnitude of kernels spike^{-1} reductions from year to year. Generally, the reductions were largest in 1989, followed by 1987 and 1988. However, temperatures in the seven day period following ethephon application, the period over which most ethylene release would be expected to occur (Lurssen, 1982), were highest in 1987, followed by 1988 and 1989. Evidently, other environmental factors also affected the magnitude of the effect of ethephon on kernels spike^{-1}.

While differential cultivar responses to ethephon have been observed (Simmons et al., 1988; Dahnous et al., 1982), and were expected in this study based on prior experience with the two cultivars (Bahry, 1988; Entz, 1988), only slight evidence of cultivar differences emerged

in this study, in which Argyle barley grown at 300 plants m^{-2} in 1988 exhibited slightly greater sensitivity to ethephon's gametocidal properties. The underlying physiological mechanisms of differential cultivar responses to ethephon do not appear to be understood; however, such differences are ultimately manifested in differing effects on individual yield components such as kernels $spike^{-1}$, and spikes $plant^{-1}$, for which slight evidence of differential cultivar response has also been presented (chapter five).

Reductions in kernels $spike^{-1}$ for individual shoots caused by ethephon were reflected in reductions in contributions to kernels $plant^{-1}$ for those shoots. Ethephon caused large reductions in kernels $plant^{-1}$ contributed by individual shoots barley grown at 100 plants m^{-2} in 1989, because both kernels $spike^{-1}$ and spikes $plant^{-1}$ (chapter five) were reduced. Despite the increase in total kernels $plant^{-1}$ caused by ethephon in 1987 at the low plant density, yield $plant^{-1}$ was not affected by ethephon because kernel weight was also reduced by ethephon.

The effects of ethephon on kernel weights in this study were inconsistent, being negative, nil, and positive in 1987, 1988, and 1989, respectively. The reduction in overall average kernel weight in 1987 was partly due to the presence of late appearing tillers with relatively lower kernel weights, but the reduction was still apparent even when only shoots which appeared before ethephon application were considered. Because ethephon also promoted the appearance of tillers while inflorescences on early shoots were at a beginning stage of kernel development in 1987, a possible explanation for the reduced kernel weights observed is that developing kernels were in competition with dependent tillers for photosynthate, a possibility which is the subject

of research presented in chapter seven. Supporting evidence is provided by Kirby and Jones (1977) and Chafai El Alaoui et al. (1988) who found that removal of emerging tillers resulted in increased kernel weights for main stems. With relatively fewer late tillers appearing after ethephon treatment in 1988, developing kernels were not subjected to the same level of competition, and therefore, kernel weights were not reduced by ethephon.

Explanation for the increased kernel weights observed with ethephon treatment in 1989 is more complex, since ethephon promoted late tillering to a similar extent as in 1987 (chapter five). Three factors may have contributed to kernel weight increases in 1989. First, although lodging occurred in both years, the prevention of lodging by ethephon was most pronounced in 1989 (lodging was more general in 1987 because of greater severity of lodging events), and the reduction of lodging may result in kernel weight increases (Foy and Witt, 1987; Simmons et al., 1988); second, available nitrogen after summerfallow was higher in 1989 than 1987 (chapter three), possibly limiting photoassimilate availability in 1987 compared with 1989 (higher kernel weights and yields in 1989 compared with the other two years were likely due to greater nitrogen availability and more favourable early season moisture and temperature conditions); third, ethephon caused the senescence of some early shoots with their heads in the boot stage, and transfer of carbon assimilates from these senescing tillers to the remainder of the plant (Lauer and Simmons, 1988) may have resulted in a less competitive situation between developing inflorescences and late tillers.

Reduced kernels spike^{-1} and kernel weight with ethephon affected both low and high plant densities, while compensatory tiller growth occurred primarily at the low plant density. Overall grain yield was either reduced by ethephon, typical at the high plant density, or was not affected, typical at the low plant density because of the greater tendency for increased spikes^{-1} to compensate for decreased kernels spike^{-1} and/or kernel weight. Despite increased kernel weights and promoted tiller emergence and spike development in 1989, absolute grain yield of barley grown at 100 plants m^{-2} was reduced due to reduced kernels spike^{-1} and the complete senescence of some early shoots (chapter five); however, combine harvestable yield tended to be increased for ethephon treated barley compared with untreated barley, because of reduced lodging (chapter four).

The increased lodging resistance conferred by ethephon is attributed to reduced plant height (Brown and Early, 1973; Entz, 1988; Neenan and Spencer-Smith, 1975) and perhaps increased straw strength through increased dry matter accumulation per unit length (Selga et al., 1985), although this increased accumulation appears to be in the form of non-structural carbohydrate (Knapp et al., 1987). The studies presented here suggest that the decreased weight carried on a stem due to reduced kernels spike^{-1}, and to a lesser extent reduced kernel weight, may also make a considerable contribution to lodging resistance.

In this study, ethephon consistently reduced kernels spike^{-1} in treated barley, and sometimes reduced kernel weight. These negative effects were only partially compensated by the promotion of late tiller emergence and spike development. Where severe lodging can be anticipated based on knowledge of growing conditions, the use of

ethephon may reduce lodging and increase harvestable grain yield despite reductions in kernels spike^{-1}, kernel weight, and absolute grain yield. However, where the risk of lodging is unknown or is not high, the use of ethephon as an insurance against the possibility of lodging can not be advised given the risk of yield reductions under Western Canadian growing conditions.

7. ASSIMILATE PARTITIONING BETWEEN MAIN STEM AND LATE-EMERGING TILLERS IN BARLEY TREATED WITH ETHEPHON.

7.1 Abstract.

Ethephon used for lodging control in cereal crops has been observed to promote the growth of tiller buds. This study was conducted to determine if changes in photoassimilate partitioning could explain the promoted growth of tiller buds in ethephon treated barley, and if competition between inflorescences and late developing tillers could explain reduced kernel weights sometimes observed in response to ethephon treatment. Argyle barley was grown in the field in 1989, and at 3, 10, and 21 days after ethephon application at GS 45, $^{14}CO_2$ was applied to the flag and penultimate leaves of both control and ethephon treated plants; plants were harvested 24 hours later. At three days after ethephon application, more ^{14}C-assimilate was found in the central and basal internodes and tiller buds in ethephon treated plants, while less was found in the peduncle and the penultimate internode, and to a lesser extent the inflorescence. Ten days after ethephon application, 40 percent of ^{14}C-assimilate exported from labelled leaves was recovered from late-emerged tillers on ethephon treated plants, with reduced recovery from the peduncle and penultimate internode and the central internodes, compared with control plants. By 21 days after application, most exported ^{14}C-assimilate was recovered from the infloresence in both control and ethephon treated plants, and the late-emerged tillers on the latter accounted for only five percent of the activity recovered. The study demonstrated that enhanced photoassimilate availability in the stem below the penultimate leaf makes an important contribution to late tiller bud growth in ethephon treated plants, and that enhanced

availability of assimilate may be due to the reduced requirement of elongating internodes higher on the plant. The study also demonstrated that late-emerged tillers depend heavily on the main stem for assimilates during their early growth; the reduced assimilate requirement of elongating stems provides for most of the necessary assimilate, but there may also be some competition between developing inflorescences and late tillers leading to kernel weight reductions with ethephon treatment.

7.2 Introduction.

When applied to cereal crop plants at the boot stage (Zadoks GS 41-45), the plant growth regulator ethephon inhibits elongation of the uppermost several internodes of the stem, resulting in shorter plants which are more resistant to lodging (Brown and Early, 1973; Entz, 1988). Yield components are affected by ethephon application, with promoted appearance of late-emerging tillers (Hill et al., 1982; Netherlands, 1989), increased spikes plant^{-1} (Bahry, 1988; Morena et al., 1988; Simmons et al., 1988) and decreased kernels spike^{-1} (Bahry, 1988; Simmons et al., 1988) being reported. Kernel weight increases have been observed when lodging was prevented by ethephon (Foy and Witt, 1987; Hill et al., 1982; Simmons et al., 1988), while decreases are sometimes reported when ethephon was applied but no lodging occurred in comparable untreated barley (Bahry, 1988; Simmons et al., 1988).

Increased spikes plant^{-1} with ethephon application have been attributed to the promotion by ethephon of growth and survival of late-emerging tillers (chapter five). Non-growing or slow-growing tiller buds may be present in the axils of many leaves at the time when ethephon is applied sometime during the boot stage (Aspinall, 1961;

Jewiss, 1972). Johnston and Jeffcoat (1977) attributed suppressed growth and emergence of tiller buds during rapid stem elongation to competition for photoassimilates in favour of the elongating stem; tiller emergence could then resume as the flag leaf became the primary supplier for the developing inflorescence, relieving the competition for assimilates at bud sites. Such resumption of tiller bud elongation and emergence has sometimes been observed after heading (Aspinall, 1961; Kirby, 1967). The importance of stem elongation in suppression or promotion of tiller bud growth is also indicated by the work of Jewiss (1972), who reported increased tillering in wheat when elongation was inhibited with application of (2-chloroethyl)trimethylammonium chloride, but decreased tillering when elongation was enhanced with application of GA_3.

Plant growth substances also appear to contribute to the outgrowth of tiller buds. The application of the auxin inhibitor 2,3,5-tri-iodobenzoic acid (TIBA), or the destruction of the apical meristem led to tiller bud growth, while if naphthalene acetic acid (an auxin) was applied to the destroyed apical meristem, tiller bud growth did not occur (Leopold, 1949). Harrison and Kaufman (1980; 1984) found that changes in the balance of auxin and cytokinin at bud sites, in favour of cytokinin, promoted bud outgrowth: they found that gravistimulation, decapitation, and inflorescence emergence, all of which are thought to reduce auxin concentration at bud sites, promoted bud outgrowth; and ethylene was shown to inhibit transport of auxin to the bud, thus promoting bud outgrowth.

A substantial portion of ^{14}C-assimilate from the lower leaves of wheat main stems was incorporated in tiller infloresences (Rawson and

Hofstra, 1969). The removal of tillers from barley resulted in main stems with more and heavier kernels (Chafai El Alaoui et al., 1988; Kirby and Jones, 1977). Removal of green leaves from barley main stems decreased tiller dry weight (Aspinall, 1963). When young leaves were removed from wheat main stems, tiller bud outgrowth was promoted, tiller senescence was delayed, fewer tillers senesced, and tillering resumed after heading (Laude, 1975). These results demonstrate that tillers depend on main stems for early growth, and compete with young leaves and the main stem inflorescence for limited assimilate resources, suggesting the possibility that reductions in kernel weight with ethephon treatment of barley may be due to competition with developing tillers promoted by ethephon.

The objectives of this study were to determine if the application of ethephon to barley results in enhanced availability of photo-assimilate to tiller buds thus promoting their growth, and to determine to what degree competition between developing grain and late tillers could serve to explain the reductions in kernel weight often observed with ethephon application.

7.3 Materials and Methods.

Argyle barley was sown in plots on May 12, 1989, at a rate giving a plant stand of 300 plants m^2, using cultural practices given in chapter three. This high density was used to obtain plants which were relatively simple morphologically, consisting of only a main stem, one or two dead tillers, and one or two non-emerged tiller buds at the time of ethephon application. Half of the plots, randomly selected, received ethephon at Zadoks growth stage 45. At 3, 10, and 21 days after ethephon application, 6-8 plants were selected from an ethephon treated plot and from an untreated plot for labelling with $^{14}CO_2$. Selection was made on the basis of uniformity with respect to degree of stem elongation, number of leaves, and number of senesced tillers; on days 10 and 21 after ethephon application, selection criteria also included the absence of late-emerged tillers on untreated plants, and the presence of similarly developed late-emerged tillers on ethephon treated plants.

$^{14}CO_2$ was generated and applied to plants by the procedures given in chapter three. The flag and penultimate leaf blades of a plant to be treated with $^{14}CO_2$ were enclosed in small polyethylene bags, and the gas containing $^{14}CO_2$ was injected into the bag. Each bag was left in place for 30 min.

Twenty-four hours after treatment with $^{14}CO_2$, plants (above-ground portion only) were taken from the field, senesced leaves and tillers were removed, and the remaining green portions were separated into the following parts: the treated leaf blades and sheaths, all other leaves, the inflorescence, the peduncle and penultimate internode including the flag and penultimate leaf nodes, the basal group of internodes and nodes to which tillers or tiller buds were attached, the remaining internodes

and nodes, any tiller buds which were present, and any late-emerged tillers which were present. The parts were dried at 90°C for 24 hours, cooled and stored in desiccators, weighed, and chopped finely.

Two subsamples weighing approximately 50-1000 mg were taken from the chopped material for each large plant part, depending on anticipated activity. The subsamples, or all material for small plant parts, were oxidized using a biological oxidizer, and radioactivity was counted using a liquid scintillation counter.

Data (dry weight and relative amount of radioactivity for each plant part) were subjected to SAS analysis of variance procedures (SAS Institute, 1982).

7.4 Results.

Total activity applied was approximately 500 and 410 kBq plant^{-1} on days 3 and 21 after ethephon application, respectively, and uncertain on day 10 because of some manometer leakage. Total activity recovered after 24 hours was 274(±70), 125(±24), and 175(±22) kBq for treatments 3, 10, and 21 days after ethephon application, respectively. Control and ethephon treated plants did not differ from each other with respect to total activity recovered.

Three days after treatment with ethephon, plants selected from control and treated plots were visually similar, having eight leaves, 2-3 of which had senesced, and 1-2 senesced tillers; however, although plant heights were not measured, it was visually apparent that the degree of spike emergence was less on treated plants than on untreated plants, with spikes fully emerged but peduncles not yet visible on untreated plants (GS 58), and spikes about halfway emerged on ethephon treated plants (GS 55). Anthesis had not yet occurred.

On the third day after ethephon application at GS 45, about 90 percent of ^{14}C-assimilate exported from the flag and penultimate leaves in control plants was recovered from the inflorescence and the upper two internodes, and most of the remaining 10 percent was recovered from the central internodes (Table 7.1). Compared with control plants, less ^{14}C-assimilate was recovered from the upper two internodes and the inflorescence (NS) in plants treated with ethephon, while more was recovered from central and basal internodes, and tiller buds. The dry weight of the infloresence and the upper two internodes was lower in ethephon treated plants than in control plants, but there was no difference in relative activity (activity g^{-1}). The dry weight of the central internodes and tiller buds was higher in ethephon treated plants than in control plants, and the relative activity in central and basal internodes, and in tiller buds was greater for ethephon treated plants. For leaves other than the flag and penultimate leaves, control and ethephon treated plants differed slightly but significantly in both relative and total activity, but did not differ in dry weight, and these leaves accounted for less than 0.5 percent of the recovered activity. Control and ethephon treated plants did not differ with respect to the weight of flag and penultimate leaves or the portion of total activity which was exported from the flag and penultimate leaves (60 and 64 percent for control and ethephon treated plants, respectively).

Plants selected 10 days after ethephon application had nine leaves, 3-4 of which had senesced, and 1-2 senesced early tillers; selected ethephon treated plants had 1-2 leaves on each of one or two late-emerged tillers, while selected untreated plants had no late-emerged tillers; spike emergence was complete on both treated and

Table 7.1. Weight and radioactivity recovered after 24 hours from various plant parts of barley fed $^{14}CO_2$ through the flag and penultimate leaves 3 days after treatment with ethephon.

Plant Part	Treatment	Weight	Relative Activity	Total Activity	Portion of Activity RecoveredΘ
		g	Bq g^{-1}	Bq	percent
Inflorescence	Control	0.3418 aΩ	279887 Ψ	93228	53.00
	Ethephon	0.3012 b	276585	83589	47.56
Penultimate and flag leaves	Control	0.3822	300957	116349	---
	Ethephon	0.3740	267585	99600	---
Other Leaves	Control	0.4453	806 b	353 b	0.22
	Ethephon	0.4161	1153 a	480 a	0.30
Peduncle and penult. internodes	Control	0.1784 a	376458	65937	37.80 a
	Ethephon	0.1475 b	367241	54170	31.89 b
Central internodes	Control	0.4315 b	30805 b	13339 b	8.29 b
	Ethephon	0.4909 a	57742 a	28422 a	17.50 a
Basal internodes	Control	0.1358	7435 b	992 b	0.64 b
	Ethephon	0.1392	24461 a	3415 a	2.31 a
Tiller Buds	Control	0.0018 b	40800 b	90 b	0.06
	Ethephon	0.0045 a	144000 a	630 a	0.44

Θ Portion of total activity recovered, excluding the flag and penultimate (treated) leaves.
Ω Means within control vs. ethephon treatment comparisons for specific plant parts are different at $P<0.05$ if followed by different letters.
Ψ Maximum counting error is 5%. For activities greater than 1500 Bq, counting error is less than or equal to 1%.

untreated plants, but a height difference of about 10 cm was obvious. Many kernels were expanded or expanding, indicating that anthesis had recently taken place in most florets (GS 67-71); spikes from control and ethephon treated plants were not inspected closely enough to detect differences in the degree to which anthesis had taken place.

About 80 percent of ^{14}C-assimilate from control plants labelled at 10 days after ethephon application was recovered from the stem, most in the upper two internodes, followed by the central internodes, and to a small extent the basal internodes (Table 7.2). Virtually all of the remaining ^{14}C-assimilate was recovered from the inflorescence. The inflorescence of ethephon treated plants contained a similar amount of ^{14}C-assimilate as that of control plants, but much less ^{14}C-assimilate was recovered from the upper two and central internodes in ethephon treated plants than in control plants. About 40 percent of the activity recovered from ethephon treated plants was found in late-emerged tillers. Tiller buds on control plants accounted for a negligible portion of the recovered activity. By weight, the inflorescence and central internodes on ethephon treated plants were non-significantly lighter than those on control plants, and the peduncle and penultimate internode were lighter on ethephon treated plants. Tillers on ethephon treated plants accounted for about eight percent of the dry weight $plant^{-1}$. Relative activity was reduced in the upper two and central internodes of ethephon treated plants compared with control plants, but the strength of tillers on ethephon treated plants as sinks is demonstrated by their draw of 40 percent of the ^{14}C-assimilate while composing only eight percent of the dry weight. For leaves other than the flag and penultimate leaves, control and ethephon treated plants did

Table 7.2. Weight and radioactivity recovered after 24 hours from various plant parts of barley fed $^{14}CO_2$ through the flag and penultimate leaves 10 days after treatment with ethephon.

Plant Part	Treatment	Weight	Relative Activity	Total Activity	Portion of Activity Recovered Θ
		g	Bq g^{-1}	Bq	percent
Inflorescence	Control	0.5812 Ω	31328 Ψ	17204	19.05
	Ethephon	0.5528	25393	13758	18.86
Penultimate and flag leaves	Control	0.3405	144433	48783	---
	Ethephon	0.3713	125090	46429	---
Other Leaves	Control	0.5116	995	502	0.60
	Ethephon	0.5277	737	386	0.57
Peduncle and penult. internodes	Control	0.3470 a	114321 a	36820 b	42.66 a
	Ethephon	0.2459 b	50751 b	12294 a	17.68 b
Central internodes	Control	0.7787	39244 a	30134 b	34.45 a
	Ethephon	0.6953	20598 b	14093 a	20.08 b
Basal internodes	Control	0.1096	25660	2776 a	3.20
	Ethephon	0.1030	20602	1989 b	2.89
Tiller(s) Φ	Ethephon	0.2192	138973	28928	39.94
	(±SD)	(±0.0575)	(±57635)	(±8955)	(±4.97)
Tillers Buds	Control	0.0024	20100	40	0.05
	(±SD)	(±0.0023)	(±16200)	(±27)	(±0.04)

Θ Portion of total activity recovered, excluding the flag and penultimate (treated) leaves.
Ω Means within control vs. ethephon treatment comparisons for specific plant parts are different at $P<0.05$ if followed by different letters.
Ψ Maximum counting error is 5%. For activities greater than 1500 Bq, counting error is less than or equal to 1%.
Φ Weights and activities recovered were combined in cases where more than one tiller had emerged. Emerged tillers were present only on ethephon treated plants; vital tiller buds were present only on untreated plants.

not differ in relative activity, total activity, or dry weight. Control and ethephon treated plants did not differ with respect to the portion of total activity which was exported from the flag and penultimate leaves (64 and 61 percent for control and ethephon treated plants, respectively).

Plants selected 21 days after ethephon application had eight leaves, 3-4 of which had senesced, and 1-2 senesced early tillers; selected ethephon treated plants had 1-2 late-emerged tillers, each with 3-4 leaves, about half the height of the main stem, and at the flag leaf or early boot stage; ethephon treated plants were approximately 10 cm shorter than untreated plants. Kernels were about midway through the grain filling period (GS 77-83).

By 21 days after ethephon application at GS 45, almost 90 percent of ^{14}C-assimilate exported from labelled leaves was found in the inflorescence of control plants, and much of the remainder was in the upper two internodes (Table 7.3). In comparison, slightly but not significantly less ^{14}C-assimilate was found in the inflorescence of ethephon treated plants, and less in the upper two internodes, but about five percent was found in the late-emerged tillers. The peduncle and penultimate internode were lighter in ethephon treated plants than in control plants, and the central internodes and inflorescence were slightly but not significantly lighter. Tillers on ethephon treated plants composed about nine percent of the dry weight. The relative activity of the major sinks, the inflorescence and the upper two internodes did not differ between control and ethephon treated plants, and although tillers still appeared to be moderately strong sinks on ethephon treated plants, their draw of five percent of the exported

Table 7.3. Weight and radioactivity recovered after 24 hours from various plant parts of barley fed $^{14}CO_2$ through the flag and penultimate leaves 21 days after treatment with ethephon.

Plant Part	Treatment	Weight	Relative Activity	Total Activity	Portion of Activity Recovered Θ
		g	Bq g^{-1}	Bq	percent
Inflorescence	Control	1.6962 Ω	63674 Ψ	105441	88.38
	Ethephon	1.6382	66256	108768	85.10
Penultimate and flag leaves	Control	0.3539	135660	48427	---
	Ethephon	0.3691	143574	52995	---
Other Leaves	Control	0.2859	372	105 b	0.10
	Ethephon	0.3697	552	209 a	0.17
Peduncle and penult. internodes	Control	0.3467 a	27476	9382 a	8.05 a
	Ethephon	0.2345 b	26880	6414 b	4.91 b
Central internodes	Control	0.6020	5043 b	3080 b	2.66
	Ethephon	0.5314	9220 a	4591 a	3.66
Basal internodes	Control	0.3084	2875	914	0.82
	Ethephon	0.3058	3622	1124	0.90
Tiller(s) Φ	Ethephon	0.3592	19042	6379	5.25
	(±SD)	(±0.1158)	(±11099)	(±4032)	(±3.83)

Θ Portion of total activity recovered, excluding the flag and penultimate (treated) leaves.
Ω Means within control vs. ethephon treatment comparisons for specific plant parts are different at $P<0.05$ if followed by different letters.
Ψ Maximum counting error is 5%. For activities greater than 1500 Bq, counting error is less than or equal to 1%.
Φ Weights and activities recovered were combined in cases where more than one tiller had emerged. Emerged tillers were present only on ethephon treated plants.

^{14}C-assimilate with nine percent of the dry weight indicates a large drop in relative strength since the observation on the tenth day after ethephon application. For leaves other than the flag and penultimate leaves, control and ethephon treated plants did not differ significantly in relative activity or dry weight, and although they did differ in total activity, their uptake of activity was almost negligible in comparison to that taken up by other portions of the plant in either case. Control and ethephon treated plants did not differ with respect to the portion of total activity which was exported from the flag and penultimate leaves (71 percent for both control and ethephon treated plants).

7.5 Discussion.

At the plant density used, late-emerged tillers (those appearing after GS 45) appeared on both control plants and plants treated with ethephon in 1989 (chapter five). More appeared on ethephon treated plants compared to untreated plants, with 0.3 and 0.1 plant^{-1} surviving to produce grain for treated and control plants, respectively. Because the objectives of this study were to understand why ethephon promoted the appearance of such tillers, and to determine the level of competition between such tillers and the developing main stem inflorescence, on days 10 and 21 after ethephon application only plants without late-emerged tillers were selected from control plots, and only plants with late-emerged tillers were selected from ethephon treated plots (on day three after ethephon application, the development of such tillers could not yet be observed, so plants were selected based only on their appearance of uniformity with one another). Because the observation of gross photoassimilate partitioning in the plant was of

more interest than partitioning from individual leaves, flag and penultimate leaves were labelled together, since together they account for most of the assimilate available to the rest of the plant during the spike emergence and grain filling stages (Patrick, 1972; Rawson and Hofstra, 1969).

Control and ethephon treated plants did not differ with respect to the weight of flag and penultimate leaves, or with respect to the amount of assimilate exported from flag and penultimate leaves. An earlier study indicated that control and ethephon treated plants did not differ with respect to photosynthetic rates in flag and penultimate leaves (Moes, unpublished data). Therefore, the following assumptions can be made in the interpretation of these results: that the total amount of ^{14}C-assimilate exported from flag and penultimate leaves is similar for control and ethephon treated plants, and therefore, that differences between control and treated plants reflect differential partitioning of the same relative amount of photosynthate.

Within three days after the application of ethephon, substantially more assimilate was present in the central and basal nodes and internodes of treated plants, assimilate apparently made available by the reduced elongation and assimilate requirement of the peduncle and penultimate internode, and perhaps by delayed or reduced infloresence development. Tiller buds on ethephon treated plants were heavier than those on untreated plants and contained a greater concentration of ^{14}C-assimilate, indicating that they were elongating and acting as assimilate sinks. While not ruling out the possibility that plant growth substances may be involved in the outgrowth of these tiller buds, these results make it clear that assimilate availability in ethephon

treated plants compared with untreated plants is important in the enhanced outgrowth of tiller buds on ethephon treated plants. Others have also observed enhanced tiller bud outgrowth with factors that enhanced assimilate availability (Johnston and Jeffcoat, 1977; Laude, 1975; Williams and Langer, 1975). The inverse relationship of tiller bud growth and main stem (or advanced tiller stem) elongation also suggests the involvement of assimilate availability in tiller bud growth (Aspinall, 1961; Jewiss, 1972; Johnston and Jeffcoat, 1977), and although tiller buds can be induced to grow with anti-auxins such as TIBA without an obvious effect on stem growth, changes in ^{14}C-assimilate availability to buds also accompany bud growth so induced (Jewiss, 1972).

At 10 days after ethephon application, late-emerged tillers on ethephon treated plants were drawing 40 percent of the ^{14}C-assimilate exported from labelled leaves. This assimilate was apparently made available by reduced elongation and assimilate requirement by the peduncle and penultimate internode, and the central internodes, with elongation of those internodes being inhibited by ethephon. The dependence of young tillers on main stems or more advanced tillers for supplies of photosynthate has also been demonstrated by others (Aspinall, 1963; Chafai El Alaoui et al., 1988; Rawson and Hofstra, 1969).

By 21 days after ethephon application, the major assimilate sink on both control and ethephon treated plants was the infloresence. Late-emerged tillers drew only a small portion of the ^{14}C-assimilate, available primarily from the reduced requirement of the shortened internodes at the top of the plant, and indicating that such tillers

were functioning nearly independent of the main stem. The demand of tillers for main stem photosynthate has been observed to decline with time (Lauer and Simmons, 1985); tillers may (Lupton, 1966) or may not (Rawson and Hofstra, 1969) become completely independent of the main stem.

On day 10, less than 20 percent of exported ^{14}C-assimilate was recovered from the inflorescence of both control and ethephon treated plants, compared with about 50 and 85 percent on days 3 and 21, respectively. A similar phenomenon was observed by Patrick (1972) in wheat when movement of assimilate from the flag leaf to the inflorescence gradually increased after the flag leaf expanded, dropped before anthesis, but increased again after anthesis such that the flag leaf became the sole supplier for the developing spike. Rawson and Hofstra (1969) also reported a large drop in the recovery of ^{14}C-assimilate from the inflorescence when wheat flag leaves were fed $^{14}CO_2$ at anthesis, compared with $^{14}CO_2$ applications at spike emergence or at early grain filling; they observed a corresponding decrease in the growth rate of the inflorescence at anthesis. The observation at 10 days after ethephon application in the present study may have been at a time when the assimilate requirement of the inflorescence was beginning to increase after a period of relatively low requirement; observation of ^{14}C-assimilate partitioning a day or two later may then have shown a much larger demand by the inflorescence. In control plants, a large percentage of ^{14}C-assimilate from the flag and penultimate leaves was recovered from the uppermost internodes, while in ethephon treated plants, much less was recovered from the uppermost internodes, and late-emerged tillers formed strong sinks.

Based on the observation that inflorescences from control and ethephon treated plants differed slightly but not significantly in weight and recovered activity, this study does not provide strong support for the hypothesis that kernel weight reductions observed with ethephon application are caused by competition between developing grain and late-emerged tillers for assimilate resources. However, the observation of little competition in this study is not sufficient cause to discard the hypothesis. In the present study, kernel weight decreases due to ethephon for main stems of barley grown at 300 plants m^{-2} were greater in 1987 than in 1989, although the reductions were not significant in either year (chapter six), and about twice as many late-emerged tillers appeared in 1987 compared with 1989 (chapter five). With the consistent negative correlation between spikes $plant^{-1}$ and kernel weight (chapter four), and the strength of late tillers as competitive assimilate sinks, it seems likely that the greater the promotion of late tillering by ethephon, the greater the reduction in kernel weight also observed with ethephon. Such reductions in kernel weight are relatively small in any case, so any competition between the inflorescence and developing tillers must be small compared with the large amount of assimilate made available for late tiller growth by reduced stem elongation in ethephon treated barley, providing a partial explanation for the failure to observe strong competition between the inflorescence and late-emerged tillers in this study.

Further explanation for the apparent lack of competition between the inflorescence and late-emerged tillers may be in altered assimilate storage and remobilization relationships between the upper internodes and the infloresence: some ^{14}C-assimilate from the flag and penultimate

leaves at and shortly after anthesis is stored in the uppermost internodes, to be remobilized and incorporated in kernels during grain filling (Rawson and Hofstra, 1969; Wardlaw and Porter, 1967). The high recovery of ^{14}C-assimilate from the upper internodes on day 10 may have reflected such storage. Perhaps differences in kernel weight between control and treated plants occur later in grain filling as stored assimilate is mobilized from the upper internodes - in ethephon treated plants, assimilate which might have constituted stored assimilate was instead drawn by the rapidly developing tillers, therefore making later grain development entirely dependent on current assimilate, and resulting in decreased kernel weights compared with untreated plants.

Other studies have shown competition for photosynthate between inflorescences and developing tillers (Chafai El Alaoui et al., 1988; Kirby and Jones, 1977). Prochazka et al. (1975) observed reduced main stem kernel weights, inhibited main stem elongation, promoted late tiller emergence, greater recovery of ^{14}C-assimilate from tillers, and reduced ^{14}C-assimilate movement to the inflorescence in winter wheat plants treated with ethephon compared with untreated plants. Although they attributed the latter observation to reduced kernels spike^{-1} which was also observed, their results do not rule out the possibility of competition between main stem infloresences and tillers. Certainly, this evidence from other studies, combined with less direct evidence from the present study, suggests that competition between developing inflorescences and late-emerged tillers does contribute to the reduced kernel weights often observed with ethephon application.

For purposes of this study, plants were grown at a density (300 plants m^{-2} that ensured that only a main stem was present for most

plants. Plants grown at a lower density produce more tillers both before and after ethephon application than those at a higher density (chapter five). Elongation of tillers present when ethephon was applied was reduced just as for main stems. It is likely that assimilate made available by the reduced elongation of the uppermost internodes of both main stems and early tillers would provide for the growth of late-emerging tillers on ethephon treated plants grown at a lower density than used for this study.

Although late-emerged tillers on these plants grown at 300 plants m^{-2} did not contribute to spikes $plant^{-1}$ or grain yield to the extent they did in 1987, the results of this study in 1989 do contribute to the general understanding of the involvement of ethephon in the promoted growth of tiller buds when conditions are such that promotion of buds occurs. Observations of vascular development, growth substance changes (including etheylene released from ethephon), and assimilate movements in the early hours following ethephon would help to further elucidate the mechanism of ethephon induced tiller bud release and the phenomenon of apical dominance in grasses in general. It is clear that changes in assimilate partitioning when plants are treated with ethephon are important in the promoted growth of tiller buds which would be far less likely to grow in the absence of ethephon. It is also clear that late-emerged tillers are heavily dependent on the main stem to support their early growth, with changed requirements of elongating stems providing the majority of the assimilate required by these tillers.

8. GENERAL DISCUSSION.

Based on these three seasons of study, and drawing on the work of others, it is possible to describe a model of the action of ethephon on barley under Western Canadian conditions. When ethephon is applied, normally just prior to spike emergence, the release of ethylene within the plant causes an inhibition of elongation of the uppermost internodes, especially the peduncle (Dahnous et al., 1982; Entz, 1988; Knapp et al., 1987; VanAndel and Verkerke, 1978). Since photosynthetic activity in exporting leaves does not appear to be affected by ethephon application (no significant difference in $^{14}CO_2$ uptake or ^{14}C-assimilate export from flag and penultimate leaves was observed), total photosynthate availability is not affected, and because the upper internodes have a reduced assimilate requirement due to reduced elongation, assimilate is drawn by alternative sinks in non- or slow-growing tiller buds. The initiation or resumption of growth in such tiller buds may be related to both assimilate availability and changes in plant growth substance balances (Johnston and Jeffcoat, 1977; Woodward and Marshall, 1988).

Depending on favourable moisture conditions, and perhaps also fertility conditions, such tiller buds may grow rapidly, initially dependent on assimilate from the main or other established stems, but with dependence decreasing to a relatively low level by about the flag leaf stage for the new tiller. The assimilate is available primarily as a result of reduced stem elongation. Tillers appearing in this way on ethephon treated plants may contribute to grain yield, but with fewer kernels spike^{-1} and lower kernel weight compared with earlier formed tillers. There is evidence from this study, and from another (Cox and

Otis, 1989), that although ethephon promotes the emergence of late tillers, it may also promote the senescence of some tillers which appeared prior to its application.

With the release of ethylene from ethephon in the developing inflorescence in the early days after ethephon application, male sterility may be induced in some florets in apical and basal positions on the inflorescence, resulting in aborted development of affected florets, in turn resulting in reduced kernels spike^{-1}. This actual reduction in kernels spike^{-1} and the lower kernels spike^{-1} contributed by late-emerged tillers both contribute to the overall reduction in kernels spike^{-1} often observed with ethephon application. The reduced kernels spike^{-1} on main stems and/or early formed tillers may also contribute to assimilate availability for late-emerged tillers.

Reduced kernel weights may be observed when barley is treated with ethephon. Part of the overall reduction in kernel weight is attributable to the contribution of late-emerged tillers with a lower average kernel weight than tillers which appeared before ethephon application. Competition for photosynthate between developing grain and late-emerged tillers might also explain part of the reduced kernel weight observed with ethephon application; evidence for such competition has also been presented by others (Prochazka et al., 1975). Assimilate which might normally have been stored in the uppermost internodes during anthesis and later remobilized to developing grain (Rawson and Hofstra, 1969; Wardlaw and Porter, 1967) is instead used for the growth of late-emerged tillers in ethephon treated barley; later kernel development then depends entirely on current photosynthate with no contribution by

previously stored assimilate, further explaining reduced kernel weights in ethephon treated barley.

If growing conditions (cultivar, fertility, moisture, and/or high wind, heavy rain, or hail events) are such that lodging is likely to occur, ethephon is effective at increasing the lodging resistance of the crop. The increased lodging resistance results from reduced plant height (Brown and Early, 1973; Entz, 1988; Neenan and Spencer-Smith, 1975) and perhaps increased straw strength through increased dry matter accumulation per unit length (Selga et al., 1985), although this increased accumulation appears to be in the form of non-structural carbohydrate (Knapp et al., 1987). The studies presented here suggest that the decreased weight carried on a stem due to reduced kernels spike^{-1}, and to a lesser extent reduced kernel weight, may also make a considerable contribution to lodging resistance.

In the three years of study, ethephon frequently caused reductions in kernels spike^{-1}, and less frequently caused reductions in kernel weight. These negative effects on grain yield were sometimes fully or partially compensated by the promoted growth of late tillers which could make a contribution to grain yield; however, the net effect of ethephon on absolute grain yield was often negative. Barley at 100 plants m^{-2} was less prone to net negative effects of ethephon on grain yield than barley at 300 plants m^{-2}, because of greater compensatory late tiller growth at the low density; however, despite apparently greater safety of ethephon use at the low density, yield was greater at the high density in two of the three years, and actual plant densities used by growers are likely nearer the high density used in this study. If lodging is prevented by ethephon, harvestable grain yield may be increased despite

decreases in absolute grain yield, as suggested by observations in 1989. The recommendation emerging from this study regarding the use of ethephon reiterates conclusions made by others (Cox and Otis, 1989; Simmons et al., 1988), that when growing conditions are such that severe lodging is likely, and current moisture conditions are adequate, the use of ethephon will reduce lodging, facilitate harvesting, and increase harvestable yield of barley grown in Manitoba.

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