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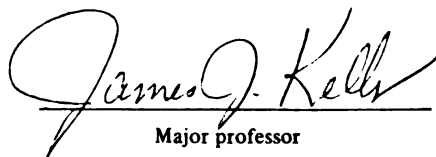
Response of 'Wakefield' Winter Wheat
(Triticum aestivum) to Dicamba

presented by

Matthew J. Rinella

has been accepted towards fulfillment
of the requirements for

M.S. degree in Crop Science


Major professor

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**RESPONSE OF 'WAKEFIELD' WINTER WHEAT (*Triticum aestivum*)
TO DICAMBA**

By

Matthew J. Rinella

A THESIS

**Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

RESPONSE OF 'WAKEFIELD' WINTER WHEAT (*Triticum aestivum*) TO DICAMBA

By

Matthew J. Rinella

Dicamba is a herbicide that is used for the control of broadleaf weeds in wheat. Typically, when dicamba is applied at proper rates and growth stages, little or no crop injury results. However, the grain yield of 'Wakefield' winter wheat is severely depressed by dicamba applied at typical rates and stages. Two years of research have confirmed that dicamba has minor effects on the number of spikelets and the seed weight of 'Wakefield'. Dicamba drastically reduces the number of normal seeds per spikelet of 'Wakefield' at typical rates and timings. Normal seeds are replaced by small, shriveled seeds that are lost during mechanical harvest. Greenhouse studies showed that untreated seed bearing plants hybridized with treated pollen source plants develop very few abnormal seeds, while treated seed bearing plants hybridized with untreated pollen source plants develop abnormal seeds. Hence abnormal pollen is not responsible for the formation of abnormal seeds.

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CHAPTER 1

REVIEW OF LITERATURE

INTRODUCTION

Dicamba is a herbicide that is used for the control of broadleaf weeds in winter wheat (*Triticum aestivum* L.) (4). Research has identified safe rates and growth stages for the application of dicamba to winter wheat (60). However, some varieties of winter wheat are injured by dicamba applied at rates and growth stages that are generally considered safe (28, 88). ‘Wakefield’, a soft red winter wheat (103), is severely damaged by dicamba applied at labeled rates and growth stages. Many efforts have been made to evaluate the effects of dicamba on wheat (20, 42, 108). The findings of some of these reports conflict. The objective of this research was to characterize the sensitivity of ‘Wakefield’ winter wheat and to compare its sensitivity to that of ‘Harus’ winter wheat.

Germination, Growth, and Development of Winter Wheat.

Germination. Winter wheat (*Triticum aestivum* L.) is planted in the fall (77, 15).

With proper moisture, oxygen, and temperature, germination quickly follows planting (96). Germination begins with swelling of the seed coat as it is permeated by water and oxygen. Once stimulated by water and dissolved oxygen, the scutellum, a specialized absorptive organ belonging to the embryo, begins to secrete gibberellic acid (99).

Gibberellic acid is absorbed by the aleurone layer, a secretory organ surrounding the endosperm. Gibberellic acid in turn triggers the release of starch degrading enzymes from the aleurone layer into the starchy endosperm of the seed (104). These enzymes break down the starch in the endosperm forming simple sugars. The scutellum, in addition to supplying its own reserves, proceeds to absorb and transport food materials (sugars and amino acids) from the endosperm to the growing embryo (56). In this manner the embryo receives the nutrition necessary for early growth and development.

Upon germination the root sheath (coleoriza) containing the primary root grows through the outer layers of the seed (pericarp) (77). About one day later the primary root breaks through the coleoriza and seminal roots begin to develop.

At the same time that the seminal roots are developing the stem is growing upward. The coleoptile, a protective leaf enclosing the first true leaf, emerges through the soil and stops growing, and the first true leaf grows through the coleoptile (98).

Growth and development. Several strategies have been developed to characterize the growth stages of wheat after emergence (54, 111, 124). Of these methods, Feeke's scale which was later modified and illustrated by Large, is the most commonly used (113).

These methods are of importance in identifying the phases in wheat development that are appropriate for particular management practices. An ability to identify the developmental stages of cereals can aid in the selection of effective and safe times for the application of fungicides and herbicides (124), and it can also assist in selecting the proper time to make rust, mildew, and other pest assessments (77).

Upon germination, when the wheat plant has one or two leaves, it is at Feeke's stage 1.

Later in the fall, if conditions are mild, the wheat plant begins to put out branches known as culms or tillers (98). Tillers arise from buds that exist on the nodes of the stem. These nodes are positioned at or just below the surface of the soil (77). The number of tillers a plant develops is dependent on several environmental factors. The number of tillers is positively correlated with soil fertility, moisture (119), and plant spacing (107), and is negatively correlated with plant density (117) and lateness of planting (44). Only tillers that are formed early in the development of the plant are likely to mature and produce seed (45). At the inception of tillering the plant is at Feeke's stage 2.

During the coldest periods of the year winter wheat goes through a phase(s) of slowed and/or arrested development. These cold periods act to vernalize winter wheat.

Vernalization is necessary for timely flowering (75).

With the warmer temperatures of spring winter cereals resume rapid growth and begin actively tillering (98). When winter wheat is fully tillered it is at Feeke's stage 3. When the tillers are formed the leaf sheaths begin to lengthen and form a pseudostem. As the leaf sheaths are lengthening the plant is at Feeke's stage 4.

Later, when the leaf sheaths become strongly erect and form a pseudostem, the plant is

at Feeke's stage 5. Following the formation of a pseudostem, the wheat plant undergoes a period of rapid development called stem extension or jointing (77). During stem extension the stem of the plant along with the developing head grows up through the pseudostem as one of the internodes begins to elongate. The node above this elongated internode becomes detectable as a swollen nob on the stem (56, 17). When this node becomes visible the plant is at Feeke's stage 6. At the same time that jointing is occurring, the head is differentiating and growing.

When a second internode elongates and a second node becomes visible on the stem, the plant is at Feeke's stage 7. This process of internode elongation and node formation continues until the last stem section, the peduncle, expands. The peduncle is the section of the stem that is directly connected to the head (98). Each expanding internode is longer than the one proceeding it, and the peduncle can account for as much as 50% of the stem length (32).

When the last leaf (flag leaf) of the plant first becomes visible, the plant is at Feeke's stage 8. When the ligule of the last leaf emerges the plant is at Feeke's stage 9. This stage is easily identified, because unlike earlier stages, no subsequent leaf tips are visible in the whorl of the plant. When the seed head is enshrouded by the sheath of the flag leaf the wheat plant has reached Feeke's stage 10. At Feeke's stage 10.1 the head is just escaping through the split in the sheath of the flag leaf, and by Feeke's stage 10.5 the head is fully emerged.

The head (spike, ear) of the wheat plant is made up of a notched main axis (rachis) which is an extension of the stem (17). The spikelets, consisting of two protective

glumes and several florets, are arranged alternately along the rachis and are attached via small branches (rachilla). As many as nine florets can develop within each spikelet, but typically only two or three florets are fertile within any spikelet (17).

Each floret has two glumes (lemma and palea). The lemma and palea surround three stamens, one pistil, and two highly branched styles (56). Flowering (anthesis) typically begins a few days after the completion of heading. The initiation of flowering is signified by the swelling of two primary leaves (lodicules) situated at the base of the ovaries (17). When the lodicules swell they force a separation of the lemma and palea and a spreading of the styles (77). While the lemma and palea are separated the filaments of the anthers elongate rapidly, reaching three times their original length in about three minutes. In this manner the anthers are pushed out of the florets. As the anthers extrude they split open on the sides and shed their pollen. Some of the pollen is shed inside the floret and some external to the floret where it can be carried by wind. Some of the pollen grains that have been shed become wedged in the stigmas. On occasion, pollen from one floret reaches the stigma of a floret on another head, but generally wheat is self-pollinated. Out-crossing has been estimated to occur in only 1 to 4 percent of florets under field conditions. Under conditions conducive to male sterility, out-crossing can occur with much greater frequency (15). About 20 minutes after lodicule swelling, the lemma and palea close and anthesis is complete (98). The initiation of flowering is called Feeke's stage 10.5.1. Flowering is complete at Feeke's stage 10.5.4.

Roughly two hours after a pollen grain is distributed it germinates and forms a pollen tube. This pollen tube, containing two reproductive nuclei, grows into the opening of the

ovule (micropyle) and discharges its nuclei into the embryo sac. One nuclei fuses with the egg nucleus to form the zygote, while the other unites with two polar nuclei forming a single nucleus. This nucleus belongs to the first cell of the endosperm (77).

Seed ripening is a gradual process that consists of several stages. In the watery-ripe stage the seed is growing quickly. This increase in size is due to rapid cell division in both the endosperm and the embryo. During the milky-ripe phase a white milk-like liquid can be squeezed out of the seed. By completion of the milky-ripe phase the embryo is fully developed. When the seeds of a plant are in the milky stage the plant is at Feeke's stage 11.1. Seed is at the mealy-ripe stage when the contents of the seed take on a meal-like or doughy consistence. When the contents of the seed have attained this soft, dry stage, the plant is at Feeke's stage 11.2. By the fully-ripe stage the plant is completely yellow and the seed is firm with the endosperm having a starchy texture. The wheat plant is now at Feeke's stage 11.3. The final stage of the wheat plant is referred to as the dead-ripe stage. The plant is dry and brittle and the seed is very hard. When the seed is ripe for harvest the plant is at Feeke's stage 11.4 (77).

Wheat Production in the Midwest.

Winter wheat is preferred in the Midwest because it matures earlier and generally yields better than spring wheat. Early maturity is considered advantageous because wheat is exposed to damaging diseases for a shorter period of time (76). Early maturity also prevents conflicts between wheat harvest and the harvest of other crops such as corn and soybeans.

Planting. Winter wheat is sown from the middle of September to the middle of

October in the Midwest with recommended seeding dates falling earlier in the northern parts and later in the southern parts of the region (84). Planting is delayed to avoid feeding damage by the Hessian fly maggot (*mayetiola destructor*), which is one of the most damaging of the numerous arthropod pests of wheat (23). Some pests and cultural problems are favored by early planting while others are advantaged by later sowing. Selection of a seeding date can be viewed as a balancing of several perils, but it is nonetheless a valuable management tool (74). Wheat often follows soybeans as part of a rotation (87). Soils, following soybean, harvest are typically loose and require minimal tillage to prepare them for wheat planting. Seed drills that can operate in untilled soil have provided an opportunity for the planting of wheat directly into soybean stubble. Herbicides may be deemed necessary to kill existing weeds at the time of planting (76). Wheat is typically planted at a rate of 60 to 120 kg/ha and a depth of 2 to 4 inches with higher rates recommended at later planting dates (75).

Fertilization. The fertilization practices utilized in wheat production are numerous in the Midwest. The quantities and types of fertilizers applied are based largely on soil tests and yield goals (76). Nutrients are typically applied in the spring due to concerns of nitrogen loss. Occasionally applications are split between fall and spring. Nitrogen is usually the limiting nutrient in wheat production with applications of phosphorus, potassium, and other nutrients occasionally deemed necessary.

Harvest. Winter wheat is usually harvested with a combine in mid to late summer. Harvest is the most critical operation in the growing of cereals. By the time a wheat stand matures it has received many inputs, and return on investment hinges on a successful

harvest (102). Weather conditions at harvest should be dry, and the crop should be ripe. Combines can only operate efficiently when the crop is ripe and dry. Successful storage of grain is also favored by a dry crop (102).

Weed Competition and its Effects on Cereals.

Competition. Weeds compete with cereals for nutrients, moisture, light, and space (77). Low yields can result from this competition or from allelopathy (10). Yield is often not directly proportional to weed numbers. Relative crop and weed emergence is of primary importance in determining the impacts of a weed infestation on yield (91).

Crops and weeds have similar nutrient requirements and differ only in the specific amounts of nutrients required for optimum growth (126). Because they are needed in large amounts and because they are often the limiting factor for plant growth, phosphorous and nitrogen are the two plant nutrients most often considered in competition studies. However, it is believed that competition for any vital plant nutrient can occur (127). Whether fertilizer favors the crop or the weed is a question of some debate (126). At least one case has been documented in which fertilizer has increased weed growth to such an extent that the crop experienced increased competition (64).

Like crop plants, weeds use large amounts of water. On a plant per plant basis some weed species require much more water than the crop species in which they grow. It has been estimated that one mustard plant removes four times as much water from the soil as one oat plant (2).

Light intensity can be a major factor affecting plant growth. Shading of soil and weeds by a crop can reduce weed competition (36). A competitive advantage is given to plants that have their leaves positioned in a way that maximizes light interception (2).

The physical positioning of leaves is more critical than total leaf area in predicting the outcome of competition (126).

Effects of weeds on yield components. Weeds can affect many yield components of cereals. Scragg et al. (91) observed that competition from wild mustard (*Sinapis arvensis*) reduced head number but had no effect on the head or seed weight of barley. Similarly, Farahbakhsh et al. (34) found that the main effect of wild-oat (*Avena fatua*), black-grass (*Alopecurus myosuroides*), and common chickweed (*Stellaria media*) on wheat yield was on the number of fertile tillers per plant. Teer (67) reported that the yield component of spring barley that was most affected by weed competition was the number of seeds per head. It has been shown that the weight of 1000 seeds of barley can be reduced by shading (67).

Effect of weeds on seed quality. Weeds can have many undesirable effects on cereals in addition to causing yield reduction. Grain that contains a large amount of weed seed is worth less money when sold. Weeds like wild garlic (*Allium vineale*) can impart an off-flavor to grain products. Weeds can interfere with harvesting and can raise the moisture content of grain (10).

History and Properties of Dicamba.

History. Zimmerman and Hitchcock (128) first reported that the substituted benzoic acids had growth-regulating properties in 1942. The herbicidal properties of 2,3,6-TBA (2,3,6-trichlorobenzoic acid) were first evaluated in field experiments in England and the United States in 1948 (50). Dicamba (3,6-dichloro-*o*-anisic acid) differs from 2,3,6-TBA only in that it has a methoxy group at the number 2 position instead of a chlorine.

Dicamba was developed by Velsicol® and first appears in a North Central Weed Control

Conference publication in 1959 under the name Velsicol B (9). In 1961 it was referred to as Banvel D, and by 1963 it assumed its current name in the North Central Weed Control Conference literature (3, 6). Later, Sandoz Agro® attained the rights to dicamba before selling them to BASF®. Dicamba is registered under the trade name Banvel® for the control of broadleaf weeds in corn, sorghum, small grains, and other crops. The maximum rate of Banvel® recommended in winter cereals is 0.14 kg ai/ha. Another formulation containing dicamba is registered as Clarity® for use only in corn (4, 5).

Site and mode of action and broadleaf weed symptoms. The mode of action of substituted benzoic acids such as dicamba is similar to that of 2,4-D (2,4-Dichlorophenoxyacetic acid) (63). These herbicides alter hormone balance and protein synthesis which results in abnormal growth of plants. Stem twisting (epinasty), callus tissue development, leaf malformations (cupping, crinkling, parallel veins, leaf strapping), and plant death often occur in broadleaf plants as a result of exposure to these herbicides (40).

Selectivity of dicamba. Chen et al. (20) studied the response of cucumber (*Cucumis sativus* L.) , a susceptible species, and wheat to four auxin-like herbicides. All of the herbicides increased the DNA and protein content of the roots of cucumber and wheat with the greatest increase occurring in cucumber. The greatest difference in the response of the two species was in the effect on RNA levels. Increasing concentrations of all four herbicides decreased RNA levels in wheat and increased the levels in cucumber. It appears that auxin-like herbicides make more of the DNA template available for transcription and thus increase RNA production in cucumber. Two studies have suggested that the increase in RNA levels of susceptible species is due to the uncoiling of

nucleohistones. The uncoiling of DNA nucleohistones facilitates enhanced transcription (19, 11). The herbicides increased the protein per unit RNA of wheat. Conversely, the protein per unit RNA of cucumber was 50% lower after treatment. This suggests that the extra RNA produced in susceptible plants may be faulty and incapable of coding for proteins. It is also possible that the aberrant RNA competes with normal RNA with a resultant synthesis of abnormal proteins. These abnormal proteins may be responsible for the distorted growth associated with dicamba. A later study showed that the incorporation of ^{14}C -leucine into protein in cucumber roots was decreased 70% 10 hr after treatment with dicamba (19).

Chang and Vanden Born (18) found that dicamba was absorbed more rapidly and completely by Tarany buckwheat (*Fagopyrum tataricum* L.) and wild mustard (*Sinapis arvensis* L.), two susceptible species, than by wheat and barley. More dicamba was translocated out of treated leaves of Tarany buckwheat and wild mustard than wheat and barley one or more days after treatment. Metabolism of dicamba occurred in all four species but not at the same rate. Dicamba was metabolized more slowly in Tarany buckwheat and wild mustard than in wheat and barley. A major metabolite (5-hydroxy-3,6-dichloro-*o*-anisic acid) was common to all four species. A minor metabolite (3,6-dichlorosalicylic acid) was present in wheat and barley but not in the other two species. These results suggest that differences in the sensitivity of these species can be explained by a combination of uptake, translocation, and metabolism.

Quimby and Nalewaja (83) submerged leaf sections of wheat and wild buckwheat (*Polygonum convolvulus*), a susceptible species, in a dicamba solution and found that differences in the susceptibility of the two species could not be explained by differences

in uptake. ^{14}C -dicamba accumulated in the meristems of wild buckwheat but not in young tillers of wheat. The main culms of wheat conjugated and/or metabolized ^{14}C -dicamba more rapidly than the meristems of wild buckwheat. These results suggest that differences in tolerance between the two species can be attributed to translocation and metabolism.

Metabolism. Broadhurst et al. (16) found that there was no free dicamba remaining in wheat plants 18 days after treatment. A small amount of conjugated dicamba remained after 29 days. 5-hydroxy-2-methoxy-3,6-dichlorobenzoic acid was the major metabolite (90%) after hydrolysis. 3,6-dichlorosalicylic acid and the parent compound were minor metabolites after hydrolysis.

Differential Sensitivity of Wheat Cultivars to Herbicides.

The selectivity of a herbicide between a weed and a crop is never absolute. In addition to environment and crop stage, the genetic makeup of the crop is also a factor (14, 21). Differences in the response of cereal varieties to herbicides are common. The first reports of varietal sensitivity did not occur with a herbicide but with the insecticide DDT. Shortly thereafter, differences in the response of some barley varieties to one of the first wild-oat (*Avena fatua*) herbicides (barban) and slight differences in the sensitivity of cultivars of cereals to 2,4-D became evident. With the development of the substituted urea herbicides (chlortoluron and metoxuron) for the control of black-grass in Europe the number of reports of differential sensitivity increased. Some wheat varieties tolerate four times the recommended dose of chlortoluron with only slight yield suppression while other varieties suffer considerable injury from the standard rate (116). Since the time of these early reports the differential sensitivity of cereal cultivars to

numerous classes of herbicides has been studied (114, 69, 101, 118, 115, 100, 68, 58, 71, 59). Particular attention has been paid to the growth regulator herbicides dicamba and 2,4-D (28, 86, 88, 106, 85, 35, 81, 43, 24, 52, 12, 51, 31, 46, 79, 95, 120).

Herbicide tolerance testing. As the number of cases of differential sensitivity increased, widespread testing of cultivars for sensitivity to herbicides began. The responsibility for testing crop tolerance is often unclear or unexcepted (110). It is the responsibility of the plant breeder to develop new varieties of cereals that have high yield potential and seed quality. It is important that these varieties produce acceptable yields over a wide range of environmental conditions and show adequate resistance to insect, disease, and other hazards to which they may be exposed. Whether herbicide tolerance is a criteria with which plant breeders should be concerned is debatable. It can be claimed that breeders should produce varieties that are tolerant to the herbicides to which they are subjected, and conversely, it can be argued that it is the duty of agrochemical companies to ensure that their herbicides do not injure the crops to which they are applied (58).

Agrochemical companies typically test their herbicides on currently used varieties and sometimes a few that are nearing release. Plant breeders conduct limited testing of new varieties with widely used herbicides (110). When contemplating the regularity of occurrence of problems with particular combinations of herbicides and varieties, it becomes evident that these screening programs are insufficient. It would be highly impractical to evaluate every herbicide/variety combination, but a testing procedure that examines the combinations that are considered most dangerous is advisable (115).

A wide margin of safety between the amount of herbicide required for acceptable weed control and the amount necessary to cause crop injury is critical (118). Identifying

safe combinations and earmarking potentially dangerous ones can be difficult. Crop injury is a notoriously variable phenomenon (108). Damage from herbicides is not easily predicted, and it is often associated with atypical growing conditions (115).

Environmental factors such as temperature, precipitation, and soil type can have a profound impact on the response of a crop to a herbicide. Often one year of testing at one location is not enough to gauge the safety of a variety/herbicide combination (35).

Conversely, several seasons may pass before conditions arise that favor crop injury (116).

This is distressing, because a particular cultivar can become popular and widely distributed before a problem arises.

Herbicide screens typically consist of cultivars planted in long narrow rows in one direction and herbicides cross-applied in the other direction. Usually these studies are not replicated and only visual injury is assessed. These simple screens expose major varietal differences in herbicide tolerance, but a less dramatic effect is often better measured in replicated yield trials (115). Herbicides are often applied at multiples of the recommended dose to mimic the effect they would have in years when the environmental conditions favor crop injury. The assumption that a high rate of herbicide simulates what occurs under conditions of extreme herbicide activity is imperfect, but it is a practical alternative to repeating experiments in several years and/or several locations (110). If a variety tolerates a herbicide applied at three or four times its normal rate it is reasonable to assume that the combination is safe. If injury occurs from the single dose then the variety is classified as sensitive. Varieties that operate between these two extremes require more critical testing to establish if crop safety is adequate (116).

The detection of cases of mild sensitivity to herbicides are of some importance. It has

been shown that many growers in parts of England are unlikely to lose yield by not applying herbicides to their cereal crops for one year (33). Any benefit from the use of a herbicide can be lost if the herbicide even slightly injures the crop.

The frequency and magnitude of differences in the response of cereal varieties to herbicides varies with the particular herbicide. Fiddian (35) reported on the effects of different herbicides applied to 17 winter wheats, 38 spring wheats, 30 spring oats, and 58 spring barleys. Differences in the response of cultivars to MCPA and 2,4-D were small. Differences in the response to mecoprop and 2,3,6-TBA may be of practical importance, and there were great differences in the response of varieties to barban. Sarpe et al. (86) found that 2,4-D and dicamba caused injury to some varieties of wheat when applied late, while bromofenoxim was tolerated by all varieties regardless of the growth stage at the time of application. Snape et al. (101) reported that wild populations of emmer wheat were polymorphic for their response to chlortoluron and metoxuron, while all of the populations that were studied were resistant to difenzoquat.

It has been suggested that strong varietal differences in tolerance are not likely to stem from differences in plant structure or differences in the uptake and translocation of the herbicide in the plant (116). It is believed that the tolerance mechanisms by which cereals avoid injury include deactivation of the herbicide, inability to change the herbicide to its active form, and differences in the site of action.

Genetic studies have revealed that many differences in the tolerance of varieties to herbicides are controlled by one or two major genes, and therefore, in these cases the characteristics are simply inherited (116). Herbicide sensitivity that is simply inherited can be tracked in breeding programs. This allows breeders to avoid susceptible lines if

materials that are otherwise similar are available. If plant breeders are aware that they have released a sensitive line they are able to issue warnings about the possibility of herbicide damage (59). When assessing the value of potential varieties, it is important that breeders are aware that susceptibility to a herbicide may have been bred into a particular line. Many potentially valuable varieties may have been disregarded because they were sensitive to the herbicide used in the selection plot (110).

Testing of cereal varieties for tolerance to dicamba. Edwards and Miller (28) applied dicamba + MCPA (0.07 + 0.14 kg ai/ha) at the 3.5 to 5-leaf stage and the 6 to 7-leaf stage to 10 varieties of spring wheat. The yield reductions ranged from 6% to 24% when averaged across application timings. With yield reductions of 6% at the 3.5 to 5-leaf growth stage and 41% at the 6 to 7-leaf stage, 'Waldron' proved to be the most sensitive of the varieties studied. The most tolerant variety was 'Coteau'. Its yield was reduced 6% at the 3.5 - 5-leaf growth stage and 5% at the 6 to 7-leaf stage.

Schroeder and Banks (88) evaluated the sensitivity of several soft red winter wheat varieties to dicamba. Dicamba was applied at 0.14 and 0.21 kg ai/ha at Feeke's stage 3 and 4. 'Coker 916' treated at Feeke's stage 4 with 0.21 kg ai/ha of dicamba yielded 14% lower than its control, while the yield of 'Coker 983' and 'Stacy' was not significantly affected by any treatment. At another location, dicamba applied at Feeke's stage 4 reduced the yield of 'Florida 302' 16% below its untreated control when applied at a rate of 0.14 kg ai/ha. The yield of 'Florida 302' was reduced 43% below its control with the 0.21 kg ai/ha rate at this same growth stage and location. 'Florida 301' and 'Coker 983' were not significantly affected by these treatments.

Tottman (106) evaluated the safety of a mixture of dicamba + 2,36-TBA + MCPA +

mecoprop (0.10 + 0.14 + 0.56 + 0.84 kg ai/ha) on three varieties of wheat. Ear dry weight was calculated as a mean that resulted from 10 treatments made 3 to 4 days apart between Feeke's stage 4 and 10. The treatment applied at Feeke's stage 7 reduced the yield of 'Maris Ranger' and 'Maris Huntsman' 20% and 40%, respectively, while having no effect on the yield of 'Capelle'. The injury in this study appeared to be caused by dicamba. In a second study, dicamba (0.28 kg ai/ha) significantly reduced the ear dry weight of 'Maris Ranger' (33%) and 'Maris Huntsman' (17%) . The ear dry weight of 'Cappelle' was not significantly affected by any treatment.

Robison and Fenster (85) evaluated 12 herbicide treatments applied to five cultivars of winter wheat. Dicamba was applied at 0.14 and 0.21 kg ai/ha to wheat that was at Feeke's stages 1,2, 9, and 10.5. The yield of 'Guide' was reduced 14% at the lower rate and 24% at the higher rate. The yield of 'Scout' was not significantly affected by the 0.14 kg ai/ha rate but was reduced 20% by the 0.28 kg ai/ha rate. The yield of 'Trapper' was also not affected by the lower rate, but the higher dose reduced the yield of 'Trapper' 26%. The yield of 'Lancer' and 'Gage' was not significantly suppressed by either rate.

Restrictions. The use of several cereal varieties and some herbicides has been restricted due to problems with herbicide tolerance. The application of difenzoquat, barban, metoxuron, and chlortoluron is only recommended on certain wheat varieties (115, 100). The commercial development of the spring oat variety 'Margam' was abandoned after it was discovered that it was sensitive to several herbicides (116).

Genetic basis of differential sensitivity. Lupton and Oliver (59) discovered that metoxuron tolerance is simply inherited by the progeny of crosses between varieties of resistant and susceptible winter wheat. In some crosses tolerance appeared to be

determined by a single recessive gene while in other crosses two genes seemed to be involved. Lallukka (52) studied the tolerance of eight spring barley cultivars to a mixture of dicamba, MCPA, and mecoprop. The yield decreases that occurred in the study seemed to be caused by dicamba. A genetic aspect of the sensitivity seemed apparent, with the two most susceptible varieties sharing the same parent. Snape et al. (100) were the first to locate a gene conferring herbicide resistance to wheat. It has been suggested that this gene may prevent difenzoquat from inhibiting DNA synthesis at the site of action of the herbicide (73). Other chromosomes carrying genes that mildly alter the degree of tolerance of wheat to difenzoquat were also found in this study. It was speculated that these genes may affect the retention and translocation of the herbicide.

The origin of genes conferring herbicide resistance to wheat has been explored (68, 101). Differences in the response of wild populations of emmer wheat (*Triticum dicoccoides*), the progenitor of all cultivated wheats (129), to chlortoluron, metozuron, and difenzoquat were evaluated. All populations of the wild species were resistant to difenzoquat. This was unexpected, because cultivated wheats are polymorphic for their response to difenzoquat. This suggests that susceptibility to difenzoquat is a result of cultivation. Like the cultivated species, wild emmer wheat was polymorphic for its response to chlortoluron and metozuron. Individual families responded similarly to chlortoluron and metozuron, suggesting that resistance to these herbicides is determined by the same genetic control. These results show that genes conferring resistance to chlortoluron, metozuron, and difenzoquat evolved before the domestication of wheat and not as a result of the use of these chemicals.

The effects of growth stage on cereal response to growth regulator herbicides.

The tolerance of cereals to growth regulator herbicides is highly dependent on the developmental status of the apical meristem at the time of treatment (113). There appear to be two developmental phases of cereals that are particularly sensitive to 'hormone' herbicides (105). The first phase occurs during spikelet initiation. Applications of herbicides made when spikelets are differentiating can alter cell division and development leading to malformations in the head (62). Early applications of MCPA and 2,4-D can cause abnormalities by altering the arrangement of new leaf and spikelet primordia (62, 1, 39, 53, 90). Typically this period of sensitivity ends when the spikelet primordia are clearly differentiated (111). Later applications of 'hormone' herbicides are believed to cause injury by affecting meiotic divisions in the pollen and egg mother cells (25, 57, 70, 80). These divisions usually take place when the head is approximately 2 cm in length (105). It has also been suggested that later applications of dicamba may affect the assimilate supply to the developing seed (112).

Relation of external stages of cereals to stages of apical development. When attempting to properly time the application of herbicides, it is impractical to ask growers to dissect plants and determine the developmental phase of the developing meristem. For this reason, application recommendations are based on external features that are hopefully correlated with the apical status of the crop (108). It is widely held that some stages of external development roughly correspond with stages of apical development. Usually the spikelet primordia are developed by Feeke's stage 5 (112). For this reason, applications of 2,4-D and dicamba are often made at this stage. The cell divisions that give rise to egg and pollen cells occur when the flag leaf begins to emerge and the 3rd node of the plant is detectable (Feeke's stage 8) (105). For this reason applications of growth regulator

herbicides should be avoided at this stage.

The application of 2,4-D and dicamba is recommended from the end of tillering until the beginning of jointing (40). Although this guideline has some practical merit, it remains very crude. The fully tillered stage cannot be easily defined and tillering does not accurately predict apical development (105, 111). Tottman (111) tried to correlate tiller number, leaf number, stem extension, and leaf sheath length with apical development. Studies were conducted using several varieties at three locations during three years to insure that any observed correlations would be consistent with different environments and varieties. Tiller number did not correlate well with the stage of apical development. The number of leaves on the main stem correlated only slightly better than tiller number. A reasonably clear prediction of the stage of development of the head could be made from the length of the stem. This would eliminate the need for a microscope for timing herbicide applications, but it would still require growers to dig up and dissect plants. Leaf sheath length correlated very highly with apex stage, and its measurement is very practical.

Evaluation of the safety of dicamba application timings for cereals. Much research has been conducted to identify safe growth stages for the application of herbicides to cereals (29, 108, 114, 47, 81, 66, 43, 60, 28, 86, 61, 85, 37, 55, 41, 112, 107, 105, 8, 121, 30, 27, 31, 48, 92, 41, 89, 85). Following is a review of some of the research that lead to the development of recommendations for timing applications of dicamba to cereals.

Martin et al. (60) applied 0.14 kg/ha of dicamba to spring wheat at Feeke's stage 1, 3, and 10. The experimental area was kept weed-free throughout the growing season. The yield of wheat treated at the mid-boot (Feeke's stage 10) growth stage was reduced 28%

below that of the control. The other two treatments did not significantly affect wheat yield.

Martin et al. (61) conducted another study evaluating the effects of growth stage on the fitness of herbicide treatments, but this time the focus was on winter wheat.

Applications of dicamba (0.14 kg ai/ha) were made at Feeke's stage 1, 3, and 10. The experimental areas were kept weed-free throughout the time the study was being conducted. Dicamba treatments applied at Feeke's stage 1 and 10 reduced wheat yield 12% and 13% respectively. The treatment applied at the fully tillered stage (Feeke's stage 3) did not significantly affect yield.

Friesen and Baenziger (38) conducted a field study in which they applied dicamba at 0.28 and 0.56 kg ai/ha to wheat at Feeke's stage 1, 2, 4, 5, 6, 10, and 10.5. Dicamba decreased wheat yield when applied at the last five growth stages at a rate of 0.28 kg ai/ha and at all stages when applied at a rate of 0.56 kg ai/ha at one location. Wheat yield was decreased with the 0.28 kg ai/ha rate at the last four growth stages at another location. The 0.56 kg ai/ha rate significantly decreased the yield below that of the untreated controls at the last five growth stages at this same location.

The effects of growth regulator herbicides on cereals.

Growth regulator herbicides can alter numerous morphological and chemical properties of cereals. The effects of these herbicides vary with crop growth stage, rate, and the specific herbicide. It is generally accepted that the parts of the plant that are affected are those that are being formed at the shoot apex at the time of herbicide exposure (108). It has been suggested that herbicide injury to plant structures formed long after herbicide application is caused by herbicide that is not immediately

metabolized or removed from the plant (38).

Root effects. Chen et al. (20) germinated wheat seeds in petri dishes containing various concentrations (0.01 to 100 ppmw) of 2,4-D, 2,4,5,-T, dicamba, and picloram. All four herbicides decreased root length at concentrations greater than 0.1 ppmw. With increasing herbicide concentration there was a corresponding decrease in the fresh weight of wheat roots.

Leaf effects. Tottman (108) found that very early applications of dicamba could cause the formation of leaves with fused edges (onion leafing) which impeded the emergence of subsequent leaves and the head. Similarly, the Weed Research Organization (108) observed that dicamba applied at the 7-leaf 8-tiller stage severely deformed the later leaves which prevented the normal emergence of heads. Dial and Thill (26) observed that the ester form of 2,4-D caused fused leaf margins when applied to oats at the 5-leaf stage. Many culms with abnormal leaf sheaths bore two or more panicles at harvest. Friesen and Baenziger (38) reported that bent internodes occurred when dicamba was applied at the 3-leaf stage. The bending appeared to be caused by leaf sheaths that were constricted at the nodes. With barley the constriction of the leaves was severe enough to impede the emergence of heads. Malformations in the stems and leaves of the main culms of wheat and barley occurred when dicamba was applied at 0.28 kg ai/ha at the 4-leaf stage. The same treatment at the 6-leaf stage caused the same effects in the tillers but not in the main culms.

Maturity effects. Keys (42) observed that a 0.14 kg ai/ha rate of dicamba applied at the 4-leaf stage slightly delayed the maturation of wheat. Quimby and Nalewaja (82) reported that wheat maturity was delayed by 4 and 6 days by 0.14 and 0.42 kg ai/ha of

dicamba, respectively applied at the late-tiller stage. Scragg (90) reported that uneven ripening of all cereals, and in oats, secondary growth after harvest sometimes occurred as a result of the use of “hormone” herbicides. Shaw et al. (93) found that a 0.45 kg ai/ha rate of the butyl ester of 2,4-D delayed the heading of barley by about 7 days when applied at the 2-joint stage. Woestemeyer (122) found that a 0.45 kg ai/ha rate of 2,4-D ester applied at the fully tillered and late-boot stage delayed wheat maturity by about 4 days. Phillips (78) found that 2,4-D ester applied at 0.23 kg ai/ha at the 2-joint stage delayed the development of wheat by 4 to 7 days.

Stem effects. Overland and Rasmussen (72) found that a 0.90 kg ai/ha rate of 2,4-D ester caused weakening and bending of barley stems and bending of wheat stems when applied at the early shooting stage. Scragg (90) observed that “hormone” herbicides often caused straw weaknesses. Shaw et al. (93) observed that there was a tendency for wheat to lodge when 2,4-D was applied at the fully tillered and late-boot stage. 2,4-D ester applied at 0.45 kg ai/ha 10 days before harvest caused lodging in a study conducted by Phillips (78). Tottman (52) found that a herbicide mixture containing dicamba, MCPA, and mecoprop decreased lodging by shortening straw length and causing lighter heads.

Keys (42) observed that a 0.14 kg ai/ha rate of dicamba applied at the 4-leaf stage increased the tillers per plant 14% and decreased plant height. Martin et al. (60, 61) applied standard rates of MCPA, 2,4-D, and dicamba to spring and winter wheat at the 3-leaf, fully tillered, and mid-boot stage. Several treatments reduced plant height and the number of heads per meter of row. Plant height was positively correlated with grain yield ($r=0.87$), indicating that herbicides that reduce plant height can also reduce grain yield. Quimby and Nalewaja (82) observed a decrease in the number of wheat heads per meter

of row when dicamba was applied at 0.84 kg ai/ha preemergence. Plant height was also reduced by dicamba treatments applied at preemergence, 2 to 4-leaf, early tiller, late tiller, and boot stages.

Head effects. Tottman (108) found that early applications of dicamba could cause the formation of abnormal heads. Spikelets were arranged oppositely instead of alternately on the head. Slightly later applications caused multiple (supernumerary) spikelets to be formed at some nodes, and in some cases the glumes of spikelets became fused together. Olson et al. (70) applied the butyl ester of 2,4-D to wheat and barley at several early growth stages and noted many head abnormalities such as supernumerary spikelets, elongated internodes, heads with opposite spikelet arrangement, and branched heads. The Weed Research Organization (108) observed the formation of opposite spikelets when dicamba was applied at a dose commonly used for weed control to wheat and barley with 5 leaves and 4 tillers and 7 leaves and 8 tillers. Edwards and Miller (28) reported that a decrease in the number of spikelets per head of wheat resulted from an early application of dicamba + MCPA (0.07 + 0.14 kg ai/ha). Friesen and Baenziger (38) described malformations in the heads of the main culms of wheat and barley when dicamba was applied at 0.14 kg ai/ha at the 4-leaf stage. The same treatment at the 6-leaf stage caused the same effects in the tillers but not in the main culms. A report from the Weed Research Organization (41) described darkened heads and thin ears (rat-tailing) as a result of dicamba (0.11 kg ai/ha) applied to spring wheat after the initiation of jointing. Tottman (109) applied a mixture of dicamba + 2,3,6-TBA + MCPA + mecoprop (0.20 + 0.28 + 1.12 + 1.68 kg ai/ha) to wheat with two or three nodes. Plants injured by this treatment had dark-colored heads that appeared very thin (rat-tailed).

Seed effects. Robison and Fenster (85) reported that 2,4-D amine (0.56 kg ai/ha), 2,4-D ester (0.28 kg ai/ha), and dicamba (0.14 kg ai/ha) reduced the number of seeds per head of wheat while having no effect on seed weight when applied at the boot stage. A report from the Weed Research Organization (41) described inflorescence sterility as a result of dicamba applied to spring wheat after the initiation of jointing. Martin et al. (60) found that dicamba (0.14 kg ai/ha) applied at the fully tillered stage reduced the number of seeds per head of spring wheat 15%. The same treatment decreased the number of seeds per head 27% when applied at the mid-boot stage. There was a positive correlation ($r=0.83$) between the number of seeds per head and yield. Derscheid et al. (24) reported that 0.45 kg/ha acid equivalent of 2,4-D increased the seed weight of oats when applied at the 5-leaf, tillered, heading, and milk stage. In some instances the seed weight increase was accompanied by a reduced number of seeds per head and yield. Yield was affected in a manner similar to the number of seeds per head suggesting that the decrease in seed number was of primary importance in causing the yield reduction.

Tottman (109) applied a mixture containing dicamba + 2,3,6-TBA + MCPA + mecoprop (0.20 + 0.28 + 1.12 + 1.68 kg ai/ha) to wheat with two or three nodes. The herbicide treatment reduced seed number but had its greatest impact on seed size. Affected seeds were small and shrivelled which prevented their collection via mechanical harvest. These results suggest that ovule fertilization occurred and endosperm growth was initiated, but it ceased prematurely giving rise to the small shrivelled seeds. Friesen and Baenziger (38) reported that floret sterility and abnormal seed development occurred when dicamba (0.14 kg ai/ha) was applied to wheat and barley at the 4-leaf stage in a greenhouse study. The ovaries of treated florets often collapsed, and cell size and

arrangement was abnormal. In many florets seed development had been initiated but not completed. This resulted in shriveled seeds that were referred to as aborted. Quimby and Nalewaja (82) observed an increase in seed weight when 0.14 and 0.42 kg ai/ha of dicamba were applied at the boot and flower stage. Seed weight was decreased by dicamba (0.42 kg ai/ha) applied at the early tiller stage in both years. Both the 0.14 and 0.42 kg ai/ha rate applied at the late tiller stage decreased seed weight in the first year of the study and the 0.14 kg ai/ha rate increased seed weight in the second year. Edwards and Miller (28) reported that dicamba + MCPA (0.07 + 0.28 kg ai/ha) affected two cultivars of wheat differently. 'Waldron' showed a decrease in spikelets per head and seeds per head while 'Coteau' showed a decrease in seed size when they were treated with an early application of the herbicide mixture. As a compensatory effect 'Waldron' showed an increase in seed size.

Quimby and Nalewaja (82) found that Dicamba (0.14 and 0.42 kg ai/ha) applied at the late tiller stage, and dicamba (0.42 kg ai/ha) applied at the boot stage reduced the percent germination of seeds harvested from plots when tested immediately after harvest. When retested several months later, only seed from plots treated with 0.42 kg ai/ha at the late tiller stage had reduced germination percentages. This suggests that dicamba can cause increased seed dormancy.

Protein, flour, mineral content, and baking quality effects. Shellenberger and Phillips (97) reported that 2,4-D had no effect on the mineral content and milling and baking qualities of wheat. Applications made during the early heading stage increased seed protein. Bode et al. (13) found that a 1.82 kg ai/A rate of 2,4-D increased seed protein content and decreased flour yield and baking quality of soft red winter wheat.

Klingman (49) reported that 2,4-D only caused increased seed protein content when it decreased grain yield. Martin et al. (61) applied typical rates of several herbicides to winter wheat at the 3-leaf, fully tillered, and mid-boot stage. 2,4-D ester (0.4 kg ai/ha) decreased seed protein content 20% when applied at the 3-leaf stage in the first year. Dicamba (0.14 kg ai/ha), MCPA (0.55 kg ai/ha), and dicamba + 2,4-D amine (0.14 + 0.4 kg ai/ha) increased seed protein 10% when applied at the fully tillered stage in the first year. Dicamba, 2,4-D ester, dicamba + 2,4-D amine, and dicamba + MCPA (0.14 + 0.4 kg/ha) increased seed protein 10, 10, 15, and 14 percent respectively, when applied at the mid-boot stage in the first year. Conversely, dicamba applied at the 3-leaf, fully tillered, and mid-boot stage reduced seed protein content 10, 10, and 9 percent respectively in the second year. Although seed protein content was not consistent with year, seed protein was negatively correlated with yield ($r = 0.65$) suggesting that increased seed protein content in winter wheat will be coupled with lower yield.

Cytological effects. Friesen and Baenziger (38) placed wheat and barley seeds in various concentrations of dicamba and allowed them to germinate. Cytological examinations revealed that prophase, metaphase, and anaphase proceeded normally once initiated. However, abnormal chromosome configurations indicated that dicamba interfered with normal spindle activity leading to slowed mitosis. A reduced number of dividing cells in the meristem was further evidence that mitosis was being stalled. Often polynucleate cells were found in florets that were sectioned. The ovaries of treated florets often collapsed and cell size and arrangement was abnormal. In many florets, seed development had been initiated but not completed. This resulted in seeds that were referred to as aborted. Normal cell development resumed when the concentration of

dicamba dropped below a threshold value. Tottman (52) observed that a mixture of dicamba + MCPA + mecoprop caused the formation of shrivelled seeds that contained an unidentified sugary liquid instead of starch.

Morgun et al. (65) found that while dicamba had a high genetic activity, MCPB and 2,4-DB did not cause mutations when used at concentrations that are typical for the control of weeds. For this reason it was suggested that dicamba may not be suited for use in seed production.

Chen et al. (120) germinated wheat seeds in petri dishes containing various concentrations (0.01 to 100 ppmw) of 2,4-D, 2,4,5,-T, dicamba, and picloram. All four herbicides increased DNA and protein levels and decreased RNA levels. Arnold and Nalewaja (11) applied dicamba (0.14 kg ai/ha) to wheat at the 3 to 4-leaf and late-boot stage. The RNA and protein content of wheat treated at the late-boot stage increased rapidly during the first 2 days after treatment and was further increased after 4 days. Wheat protein and RNA content did not change as a result of the treatment at the earlier stage.

‘Wakefield’ wheat. ‘Wakefield’ is a soft red winter wheat (*Triticum aestivum* L.) variety that was developed at the Virginia Agricultural Experiment Station and released in July of 1990. ‘Wakefield’ has several genes for disease resistance, lodging resistance, and high yield potential. The performance of ‘Wakefield’ in nurseries suggests that it is suited to areas outside the mid-Atlantic region where it was developed (103).

‘Harus’ wheat. ‘Harus’ is a soft white winter wheat (*Triticum aestivum* L.) that was developed at the Agriculture Canada Research Station, Harrow, Ontario and released in 1985. ‘Harus’ is a short-strawed, early-maturing, lodging-resistant, high-yielding, variety

with good disease resistance. The performance of 'Harus' was good in south and central Ontario (129).

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CHAPTER 2

RESPONSE OF 'WAKEFIELD' WINTER WHEAT (*Triticum aestivum*) TO DICAMBA

ABSTRACT

Dicamba is a herbicide that is used for the control of broadleaf weeds in wheat. Typically, when dicamba is applied at proper rates and growth stages, little or no crop injury results. However, the grain yield of 'Wakefield' winter wheat (*Triticum aestivum* L.) was depressed more than 95% in 1995 and more than 60% in 1997 by dicamba applied at typical rates and stages, while the yields of 'Harus', 'Lowell', and 'Chelsea' were not affected by these treatments. Two years of research have confirmed that dicamba has minor effects on the number of spikelets and the seed weight of 'Harus' and 'Wakefield'. Dicamba drastically reduced the number of normal seeds per spikelet of 'Wakefield' at typical growth stages in both the field and greenhouse. The seed number of 'Harus' was only decreased at late growth stages in the field. Decreases in grain yield were of the same magnitude as decreases in normal seed number. When dicamba was applied, small, shriveled seeds that were lost during mechanical harvest resulted. Dicamba had little effect on the number of sterile florets. Greenhouse studies showed that untreated 'Wakefield' plants cross-pollinated with treated 'Wakefield' pollen source plants develop very few abnormal seeds, while treated plants cross-pollinated with treated or untreated pollen source plants develop abnormal seeds. Hence, the development of abnormal seeds when dicamba is applied is not the result of abnormal pollen.

INTRODUCTION

Weeds compete with cereals for nutrients, moisture, light, and space (22). Yield reductions can result from this competition and may also occur in response to allelopathy (2). Dicamba (3,6-dichloro-*o*-anisic acid) is a growth regulator type herbicide that controls some annual and perennial broadleaf weeds in wheat (1, 2, 14, 27). Often dicamba is used when weed species are present that are tolerant to 2,4-D (26). The mode of action of dicamba is similar to that of 2,4-D (19). Dicamba alters the hormone balance and protein synthesis of broadleaf plants which results in abnormal growth. The exact sites of action of dicamba are not known and are believed to be multiple (11). Stem twisting (epinasty), callus tissue development, leaf malformations (cupping, crinkling, parallel veins, and leaf strapping), and plant death often occur in broadleaf weeds as a result of exposure to dicamba (11).

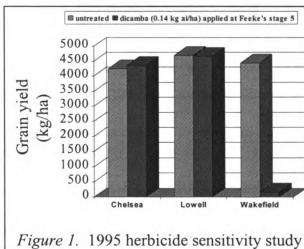


Figure 1. 1995 herbicide sensitivity study

Typically wheat is tolerant to dicamba when it is applied between the end of tillering (Feeke's stage 3) and just prior to jointing (Feeke's stage 5) (11). However, the yield of 'Wakefield', a soft red winter wheat (*Triticum aestivum* L.), was reduced over 95% by a standard application (0.14 Kg ai/ha applied at Feeke's stage 5) of dicamba in a 1995 herbicide sensitivity study at Michigan State University (Figure 1). Affected 'Wakefield' heads had a dark color and a thin (rat-tailed) appearance (Figure 2). There are reports of rat-tailed heads in the literature, but they occurred when dicamba was applied after the initiation of jointing (12, 31).

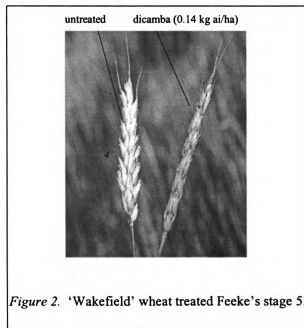


Figure 2. 'Wakefield' wheat treated Feeke's stage 5.

'Wakefield' was not the first variety to show sensitivity to dicamba. Edwards and Miller (9) showed that the grain yield of 'Waldron' was decreased more than that of nine other spring wheat varieties when dicamba + MCPA was applied at the 3.5 to 5 and the 6

to 7-leaf stage. Schroeder and Banks (27) reported on two varieties of soft red winter wheat that were moderately sensitive to dicamba applied at Feeke's stage 4. Tottman (29) evaluated the safety of a mixture of Dicamba + 2,36-TBA + MCPA + mecoprop on three varieties of wheat. Two varieties had reduced yields when the dicamba mixture was applied at Feeke's stage 7, while a third did not. The dicamba component in the herbicide mixture appeared to be responsible for the observed injury symptoms. Robison and Fenster (25) applied dicamba at Feeke's stage 1, 2, 9, and 10.5 to five cultivars of winter wheat and found that the grain yield of only one variety was affected by a typical use rate. The injury reported in these studies was not as severe as the injury that occurred with 'Wakefield', and many of the treatments were made at later stages of growth.

Growth regulator herbicides have been reported to affect cereals in many different ways. Injury symptoms vary with the particular herbicide, rate of application, cereal species and application timing. Root (5), and leaf (8, 10) abnormalities, delayed maturity (24, 34), plant height reductions (24), straw weaknesses (21, 28), and seed protein increases (18) have been described. Head abnormalities such as the development of oppositely arranged spikelets instead of placement in the usual alternate configuration, elongated head internodes, branched heads, multiple (supernumerary) spikelets at one node, and decreases in spikelet number have occurred (9, 20, 30). Increases (6, 24, 27) and decreases (9, 24) in seed weight and decreases in seed number due to floret sterility (10, 12, 31) have been reported. There have been reports of shriveled seeds as a result of exposure to dicamba and dicamba mixtures (10, 31). Friesen and Baenziger (10) referred to this condition as seed abortion.

The objectives of this research were to: 1) compare the sensitivity of 'Wakefield' and 'Harus' wheat to dicamba, 2) determine the per head grain yield component(s) responsible for the yield reductions in 'Harus' and 'Wakefield' wheat, 3) determine if dicamba causes floret sterility and/or seed abnormality in 'Harus' and 'Wakefield' wheat, and 4) determine if dicamba causes the development of abnormal pollen in 'Wakefield' wheat.

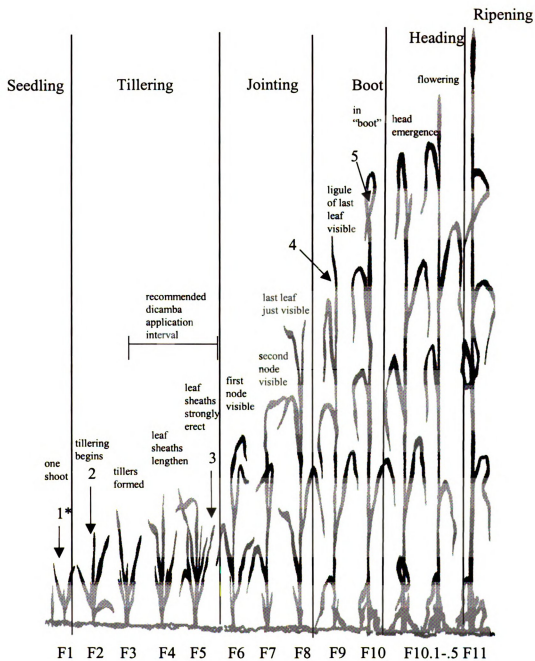
MATERIALS AND METHODS

Field study.

A field experiment was conducted at the East Lansing campus of Michigan State University in 1995-96 and a duplicate field experiment was conducted in 1996-97 to evaluate the sensitivity of 'Wakefield' and 'Harus' winter wheat (*Triticum aestivum* L.) to dicamba applied at two rates and five growth stages. The soil was a capac loam (Aeric Endoaguals, fine-loamy, mixed, mesic) with an organic matter content of 2.9% and a pH of 6.9. The soil was tilled with a field cultivator prior to planting. Nitrogen, phosphorous, and potassium were applied as recommended by soil test results. The experiments were planted on October 12, 1995 and September 27, 1996 with a seeding rate of 4.4 million seeds per hectare and a planting depth of 1.9 to 2.5 cm. Plot size was 1.5 by 3.4 m, and plots consisted of 7 rows spaced 15 cm apart. Experimental plots were bordered by plots planted with 'Harus'.

Dicamba was applied to wheat with a tractor-mounted compressed air sprayer. Flat fan nozzles (8003) and a spray pressure of 206 kPa were used to deliver 187 L/ha of a herbicide solution.

Dicamba was applied at Feeke's stage 2, 3, 5, 9, and 10 (F2, F3, F5, F9, and F10) at 0.14 and 0.28 kg ai/ha (Figure 3). The treatments were applied on April 24, May 13 and 22, and May 5 and 11 in 1996. The treatments were applied on April 15 and 26 and May



*Dicamba was applied at each numbered arrow in the field and at arrows 2, 3, 4, and 5 in the greenhouse.

Figure 3. Feeke's scale and growth stages for field and greenhouse studies.

2, 20, and 31 in 1997. When wheat first begins to develop tillers it is at F2. F3 corresponds with the end of tiller development. F5 occurs just prior to jointing when the leaf sheaths become strongly erect. F9 is marked by the emergence of the ligule of the highest leaf (flag leaf) of the plant. At F10 (boot) the spike is enshrouded by the sheath of the flag leaf and is nearing emergence.

Ten heads were collected from each plot prior to harvest in 1996 and 1997. The number of spikelets per head was counted. The heads were mechanically threshed in the first year and hand-threshed in the second year, and the number of seeds per spikelet was determined. Wheat spikelets are composed of florets arranged alternately along a tiny branch or rachilla (22). Three additional heads were collected in 1997, and the lowest two florets of each spikelet were dissected. These are the florets that produce most of the yield in wheat. The number of normal, abnormal, and absent seeds was calculated from these florets. Plots were mechanically harvested on July 28, 1996 and July 29, 1997, and the weight of 1000 seeds and grain yield were determined. Yields were adjusted to 13% moisture.

Treatments were comprised of a factorial combination of variety, application rate, and time of application. Treatments were arranged in a split-plot design where individual means were compared using a least significant difference test at the 5% level. There were treatment by year interactions for the data, so data from each year were analyzed separately.

Greenhouse study.

Greenhouse experiments were conducted to evaluate the sensitivity of 'Wakefield' and

'Harus' wheat to dicamba applied at two rates and 4 growth stages. Approximately 36 seeds of 'Wakefield' and 'Harus' wheat were planted in 10-cm square pots every seven days for several weeks. The wheat was allowed to germinate and grow for one week under greenhouse conditions conducive to wheat growth. The wheat was then placed in a cold room at 4 C to induce vernalization. After 56 days the plants were removed from the vernalization chamber and transplanted into round pots with a diameter of 10 cm. Three plants were transplanted into each pot.

Dicamba was applied to wheat with a greenhouse sprayer at a rate of 0.14 and 0.28 kg ai/ha. Treatments were made at F3, F5, F9, and F10. Plants from different planting dates were used in order to allow all treatments to be applied on the same day within each run.

Data were collected on the main culm of each plant in each pot. The number of spikelets per spike was calculated. The two basal florets from each spikelet were dissected, and the number of normal, abnormal, and absent seeds per spikelet were determined. Spikes were hand-threshed and total seed weight per spike were determined.

Treatments were comprised of a factorial combination of variety, application rate, and time of application. Treatments were arranged in a completely randomized design where individual means were compared using a least significant difference test at the 5% level. There were treatment by run interactions for the data, so data from each run were analyzed separately.

Hybridization study. Treated and untreated plants of 'Wakefield' were hybridized to evaluate the response of seed bearing plants and pollen from treated pollen donor plants to dicamba. 'Wakefield' plants were planted, vernalized, and transplanted as in the

previous study. Dicamba was applied at F9 at a rate of 0.14 and 0.28 kg ai/ha.

At the time of head emergence all anthers were removed (emasculated), and all but the two basal florets were removed from each spikelet of several spikes to prevent self-pollination. These spikes were covered with paper bags to prevent cross-pollination. At the time of anthesis, spikes were cut from plants that were not emasculated, and their stems were placed in plastic vials containing water in order to prolong spike longevity and pollen dissemination. These excised spikes were placed inside the bags containing the emasculated spikes in order to induce cross-pollination.

Treatments consisted of : 1) pollen from untreated plants crossed to plants that were emasculated and untreated, 2) pollen from treated plants crossed to plants that were emasculated and untreated, 3) pollen from untreated plants crossed to plants that were emasculated and treated, 4) pollen from treated plants crossed to plants that were emasculated and treated, 5) self-pollinated untreated plants, and 6) self-pollinated treated plants. Heads were dissected about 30 days after pollination, and the number of abnormal seeds per spikelet were counted.

Treatments were comprised of a factorial combination of application rate (untreated and 0.14 kg ai/ha), hybridization (self-pollinated and cross-pollinated), and plant type (seed bearing plant and pollen donor plant). Treatments were arranged in a completely randomized design with each treatment being replicated four times. Data were subjected to an analysis of variance. Treatment by run interactions were not significant for the two experiments utilizing the 0.14 kg ai/ha rate of dicamba, so these data were combined.

Data from experiments utilizing the 0.28 kg ai/ha rate were also combined.

RESULTS AND DISCUSSION

Field and Greenhouse study.

The fall and winter of 1995-96 were very severe from a wheat production standpoint. Early onset of cold temperatures resulted in poor vegetative growth in the fall. Prolonged periods with no snow cover and extremely cold temperatures lead to low plant density and vigor. The fall and winter of 1996-97 were more mild which resulted in good plant growth and winter survival.

Grain yield in field. Due to the similarities in the response of wheat at the two rates, only results obtained from the untreated controls and the 0.14 kg ai/ha rate of dicamba are presented in this chapter. The yield of 'Wakefield' was reduced more by exposure to dicamba than that of 'Harus' in both years, and later treatments were more injurious to both wheat varieties (Figure 5 and 6). Dicamba reduced the grain yield of 'Wakefield' 50% when applied at F10 in 1996. No treatment reduced the grain yield of 'Harus' in 1996 (Figure 5). In 1997, the grain yield of 'Wakefield' was reduced by dicamba applied at F3, F5, F9, and F10 by 57, 63, 99, and 100 percent, respectively (Figure 6). No other wheat varieties have been reported to respond this severely to a typical use rate (0.14 kg ai/ha) of dicamba (9, 25, 27, 29). The grain yield of 'Harus' treated at F10 was lower than the yield of 'Harus' treated at F3, but no treatment reduced the grain yield of 'Harus' below that of the untreated control in 1997. The superior performance of 'Harus' treated

at F3 presumably resulted from a combination of the timely removal of weeds by dicamba and an absence of crop injury. Late applications of dicamba have been shown to cause yield reductions in a number of studies (9, 25, 29). Due to the risk associated with late applications of dicamba, it is not recommended for use beyond F5 (11). The reasons for the differences in the yield response between years is not clear. There were differences in the rate of development of wheat between the two years and this may have been a factor. Additionally, the lower leaf area that was present in 1996 may have resulted in a reduction in the amount of herbicide taken up by plants.

Seed weight per head in greenhouse. Due to the similarity in the response of wheat to both rates, only results obtained from the untreated controls and the 0.14 kg ai/ha rate of dicamba are presented in this chapter. The total seed weight per wheat head of ‘Wakefield’ was consistently more sensitive to dicamba than that of ‘Harus’ in both runs of the greenhouse study (Figure 7 and 8). The seed weight per head of ‘Wakefield’ was severely reduced by every treatment in both greenhouse experiments. The reductions caused by dicamba applied at F3 and F5 were similar in the first run, as were the reductions caused by the F9 and F10 treatments. Unlike the field study, in which the yield reduction of ‘Wakefield’ was a function of growth stage at the time of application, the head seed weight reduction was severe and independent of growth stage in the second run of the greenhouse study. Head seed weight of ‘Harus’ was reduced more by dicamba exposure at F5 and F9 than F10 in the first run. This is inconsistent with results from field studies in which wheat exhibited more injury from progressively later treatments. It is somewhat surprising that a wheat variety that is tolerant to recommended applications

of dicamba in the field ('Harus') would be injured in the greenhouse. Freisen and Baenziger (10) observed that wheat was more sensitive to dicamba under lush greenhouse conditions. Head seed weight of 'Harus' was not affected by the F3 treatment, and the F5, F9, and F10 treatments caused increasingly more injury in the second run.

Seeds per spikelet in field. The number of seeds per spikelet of 'Wakefield' was reduced when dicamba was applied at F9 and F10 in 1996 (Figure 5). The number of seeds per spikelet of 'Harus' was reduced by dicamba applied at F10. The number of seeds per spikelet of 'Wakefield' was reduced by dicamba applied at every growth stage in 1997 (Figure 6). Dicamba exposure at F9 and F10 caused an almost complete loss of seeds. No single treatment significantly reduced the number of seeds per spikelet of 'Harus' in 1997. Reductions in seed number have been previously reported, but this response usually stems from high rates or late applications (9, 17, 31). The reductions in the number of seeds per spikelet of both 'Wakefield' and 'Harus' corresponded very closely to grain yield reductions.

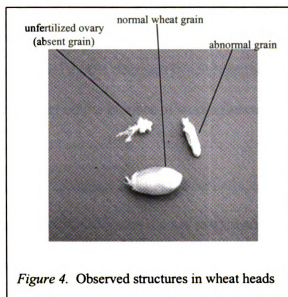
Seeds per spikelet in greenhouse. The number of seeds per spikelet of 'Wakefield' was strongly decreased by every dicamba treatment in both greenhouse experiments (Figure 7 and 8). Unlike the field study, exposure to dicamba at F5 was not as injurious as exposure at F3 in the first run. Dicamba applied at F9 and F10 caused abnormal development of almost all seed in the first run. Every treatment resulted in a reduction in the number of seeds per spikelet of 'Wakefield' by more than 90% in the second run. The number of seeds per spikelet of 'Harus' was decreased by dicamba at F5 in the first run and F9 and F10 in both runs. Seed number was not decreased by dicamba at F5 and

F9 in the field studies. Seed reduction in 'Harus' was not as sharp as that observed with 'Wakefield'. Head seed weight was highly dependent upon the number of seeds per head with both cultivars.

Spikelets per head in field. The number of spikelets per head of 'Wakefield' was not affected by any treatment in 1996 (Figure 5). There was a slight depression of the number of spikelets per head of 'Harus' when dicamba was applied at F3, F5, and F9. Spikelet primordium are typically formed by F5, so it may be that the observed reduction in spikelet number resulted from spikelets that were formed but were highly underdeveloped. The highest number of spikelets occurred when dicamba was applied to 'Harus' at F10, and this slightly compensated for the lower seed number that occurred at this growth stage. There was no significant effect of the growth stage at the time of application on spikelet number in 1997 (Figure 6). The number of spikelets per head of 'Harus' was not affected by any treatment in 1997. Reductions in spikelet number had a negligible effect on grain yield.

Spikelets per head in greenhouse. The number of spikelets per head of 'Wakefield' was not affected by any treatment in the greenhouse study (Figure 7 and 8). The spikelet number of 'Harus' was increased by dicamba applied at F3 in the first run. Multiple spikelets at single nodes resulted from this treatment. Tottman (30) reported that early applications of dicamba were capable of causing the development of supernumerary spikelets. The F9 treatment caused a 14% reduction in the number of spikelets. This decrease probably had an effect on total head seed weight. No treatment affected the number of spikelets per head of 'Harus' in the second run.

Seed weight. The weight of 1000 seeds of 'Wakefield' was slightly increased by dicamba applied at F9 and F10 in 1996 (Figure 5). Quimby and Nalewaja (24) obtained similar results when they applied dicamba at F10. These same two treatments caused reductions in the seed weight of 'Wakefield' in 1997 (Figure 6). Reductions in seed weight have been reported previously (9, 24). The seed weight of 'Harus' was not significantly affected by dicamba in either year. However, the weight of 1000 seeds of 'Harus' was highest when dicamba was applied at F10, and this may have been a compensatory response to the reduction of seed number at this growth stage.



Effect of dicamba on seed development in field. Inspection of treated heads of 'Wakefield' and 'Harus' in the field revealed normal seeds, sterile florets (absent seeds), and very small, shriveled (abnormal) seeds (Figure 4). These seeds, when dried, contained little or no endosperm and did not contribute to grain yield. Abnormal seeds of

'Wakefield' occurred when dicamba was applied at all five growth stages (Figure 9). The number of abnormal seeds increased with later applications. Dicamba caused a similar number of abnormal seeds to develop in both 'Wakefield' and 'Harus' when applied at F10, but no other application caused a large number of abnormal seeds in 'Harus' (Figure 9). The increases in the number of abnormal seeds corresponded closely with decreases in yield and harvested seed number with 'Wakefield'. This correlation was not as strong for 'Harus'. Dicamba caused 85% of the basal florets to produce abnormal seeds when applied at F10, but dicamba decreased the grain yield by only 46% at this growth stage. It appears that dicamba affected the basal florets within a spikelet more severely than the other florets. While dicamba caused an 85% decrease in the number of normal seeds in the basal florets, it only caused a 68% decrease in seed number in the other florets. Dicamba had a minimal effect on the number of sterile florets per spikelet of 'Harus' and 'Wakefield'.

The abnormal seeds were too small and light to be collected by mechanical harvest. From this it can be concluded that dicamba did not truly reduce seed number, but instead, it reduced the number of seeds that could be mechanically harvested.

Shriveled seed as a result of late applications of dicamba has been previously reported (10, 31). Friesen and Baenziger (10) referred to the condition as seed abortion. Efforts were made with a light microscope to determine if an embryo was actually present in the seeds. Embryos of the size that exist in mature wheat seeds were not present, but it was not determined if smaller or underdeveloped embryos were present. Reports indicate that growth regulator herbicides may affect meiotic cell divisions in the pollen and egg

mother cells (7, 16, 20, 23). One report suggests that dicamba that is present at the time of seed development can affect assimilate supply (32). However, seed abnormalities do not typically result from applications of dicamba made at F2, F3, and F5. It has been established that wheat metabolizes dicamba (3, 4). It is possible that 'Wakefield' does not metabolize dicamba rapidly, and shriveled seed may result from herbicide remaining in the plant at the time of gamete formation, anthesis, and seed growth and development. When late applications of dicamba are made to 'Harus', the plant does not have the opportunity to metabolize the herbicide before it causes the formation of abnormal seed. Applications of dicamba to 'Wakefield' at early growth stages may "simulate" dicamba exposure to 'Harus' at late growth stages if an appreciable amount of active herbicide remains in the plant for a long period of time. The fact that the injury symptoms are similar for both 'Harus' and 'Wakefield' supports this hypothesis.

Effect of dicamba on seed development in greenhouse. Seed development of treated plants was closely observed in the greenhouse. Pollen shed, ovary fertilization, and the early enlargement of the caryopsis appeared to be normal. When the treated seeds reached approximately one half the size of mature wheat seed, they began to appear flaccid. Squeezing of the treated seed produced a sugar-water solution. Squeezing of untreated seeds of the same size yielded a starchy substance. Tottman (15) described a similar condition when a mixture of dicamba + MCPA + mecoprop was applied to wheat. In time the affected seeds became dry and shriveled, appearing identical to the abnormal seeds that were observed in the field.

Dicamba caused the development of abnormal seeds at each growth stage in both runs

of the greenhouse study (Figure 10). Dicamba had a stronger effect on the number of abnormal seeds at the later two growth stages than at the earlier stages in the first run. Dicamba caused the replacement of almost all normal 'Wakefield' seeds by abnormal seeds at each growth stage in the second run. A large number of seeds became abnormal when dicamba was applied to 'Harus' at F5 in the first run and at the last two growth stages in both runs. An appreciable number of injured seeds developed only at F10 in the field with 'Harus'. Increases in the number of abnormal seeds coincided with decreases in the number of normal seeds and total head seed weight for both varieties. The number of sterile florets (absent seeds) was not affected by any treatment. A few abnormal seeds occurred in some untreated heads indicating that the condition could be caused by factors other than dicamba exposure.

Hybridization study.

Abnormal seeds develop in the hybridization study utilizing the 0.14 kg ai/ha rate only when the seed bearing plants were treated. (Figure 11). Pollen from treated plants did not cause the development of abnormal seeds. Self-pollinated treated plants responded similarly to plants that were treated and cross-pollinated with a treated pollen source. Surprisingly, the treatment consisting of treated plants hybridized with untreated pollen donors caused significantly more abnormal seeds than treatments in which both the pollen source plant and the seed bearing plant were treated. A clear explanation of this phenomenon is not available. Often dicamba delays the maturity of wheat (24, 34). It is possible that crosses involving untreated pollen source plants were made at different times than crosses involving treated pollen source plant. Differences in the environment

at the time of pollination may have caused the increase in the number of abnormal seeds.

When seed bearing plants were treated with 0.28 kg ai/ha of dicamba, very high numbers of abnormal seeds developed (Figure 11). Virtually no abnormal seeds developed when dicamba was not applied to pollen or plants. When treated pollen source plants were hybridized with untreated plants 13% of the seeds became abnormal. This suggests that dicamba can affect pollen if it is applied at a high rate. However, male sterility is not of primary importance in causing the development of abnormal seeds. The fact that injured pollen can cause the condition may counter the assertion that dicamba affects the assimilate supply to the developing seed. It seems unlikely that the pollen source would have any effect on the amount of nutrients available for seed growth and development. It is interesting to note that affected pollen elicits the same type of injury as affected plants.

Grain yield and the various per head grain yield components of 'Wakefield' were more sensitive to dicamba than were those of 'Harus'. Dicamba has the potential to cause drastic yield reductions in 'Wakefield' when it is applied at typical rates and growth stages, and this herbicide/variety combination should be avoided. Genetic studies have revealed that many differences in the tolerance of cereal varieties to herbicides are controlled by one or two major genes, and therefore, in these cases the characteristics can be simply inherited (33). In the future, any variety that is developed with 'Wakefield' parentage should be screened for tolerance to dicamba.

Dicamba has a very strong effect on seed morphology, but a minor effect on other

plant attributes. The injury caused by dicamba applied to 'Wakefield' at proper growth stages is in every way analogous to the injury observed in less sensitive varieties when dicamba is applied at later stages of development. Very simple screens in which wheat heads are closely examined at the time of harvest would certainly reveal sensitivity problems of this type.

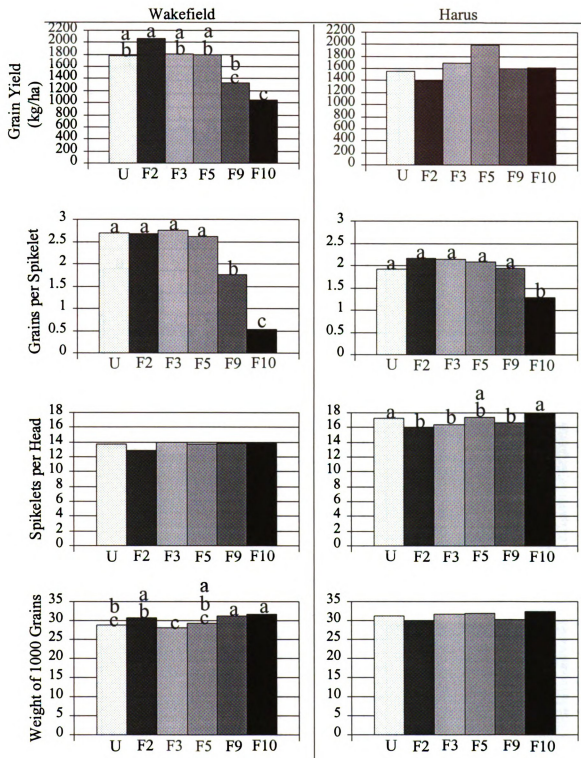
'Wakefield' was not injured by dicamba applied at F5 in the field study in 1996 but was severely injured by dicamba applied at this growth stage in 1997. Perhaps 'Wakefield' should be included in herbicide sensitivity screens that focus on dicamba sensitivity. Data that are generated in these screens in years when 'Wakefield' is not injured would be considered less reliable.

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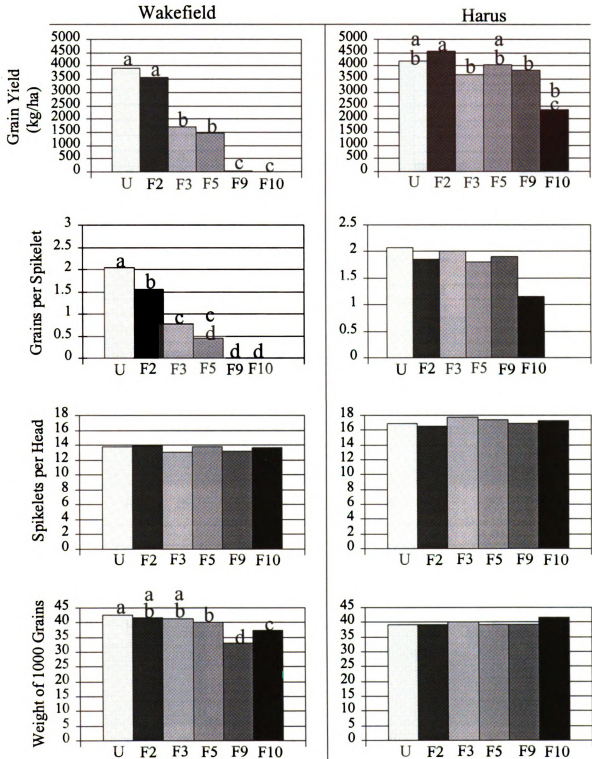
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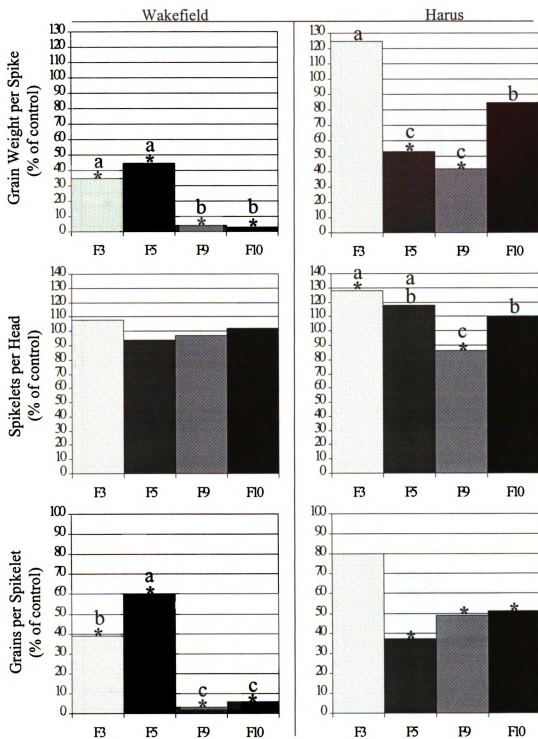
Means with the same letter are not significantly different at the 5% level

Figure 5. Effect of dicamba on grain yield and yield components in field 1996.



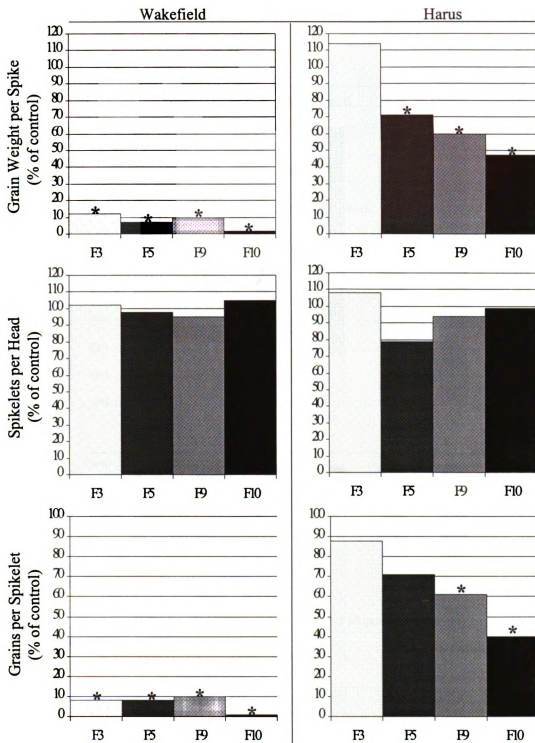
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Figure 6. Effect of dicamba on grain yield and yield components in field 1997.



Means with * are significantly different than their respective untreated control at the 5% level
 Means with the same letter are not significantly different at the 5% level

Figure 7. Response of yield components to dicamba in greenhouse run 1.



Means with * are significantly different than their respective untreated control at the 5% level
 Means with the same letter are not significantly different at the 5% level

Figure 8. Response of yield components to dicamba in greenhouse run 2.

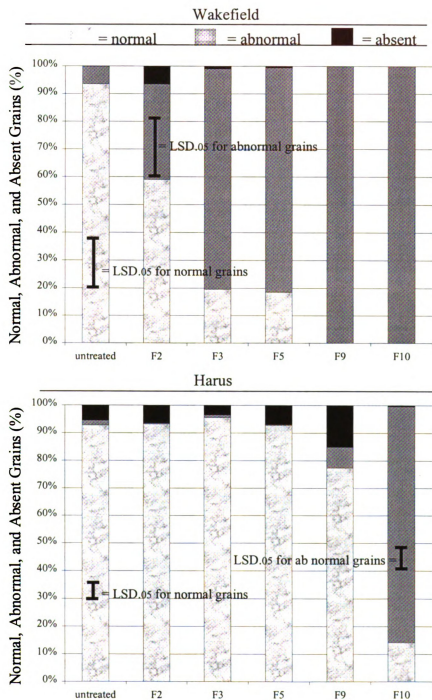


Figure 9. The effect of dicamba on seed quality in field 1997.

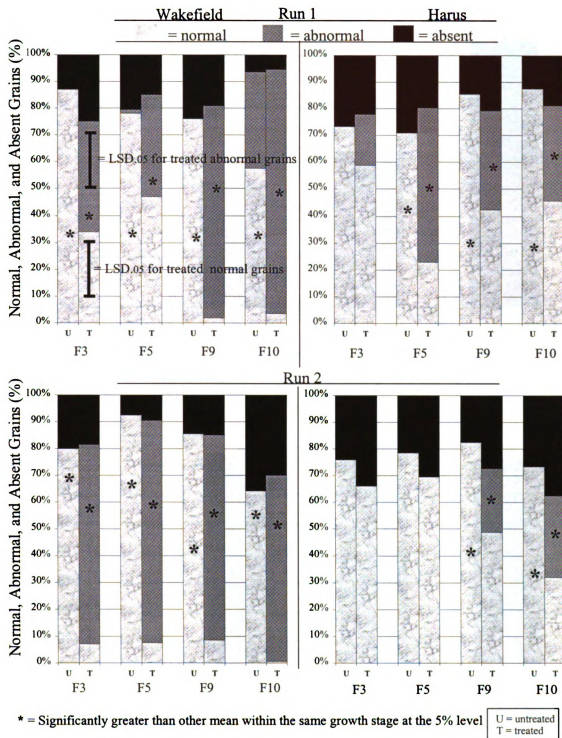


Figure 10. The effect of dicamba on seed quality in greenhouse.

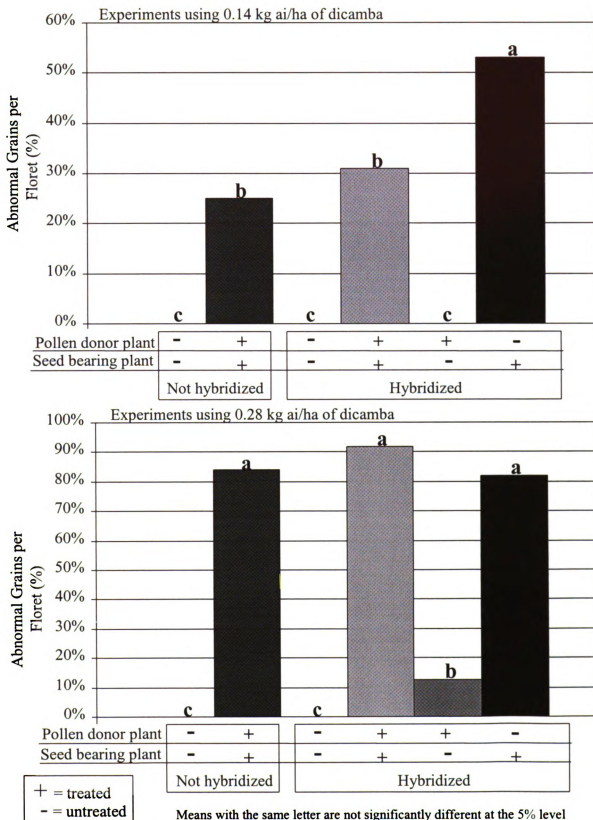


Figure 11. The effect of dicamba on seed bearing and pollen donating plants.

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