Influence of a legume covercrop on volunteer wheat, the wheat curl mite, Aceria tosichella (K.) and wheat streak mosaic virus
by Matthew Wyatt Carroll

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology
Montana State University
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Abstract:
The wheat curl mite (WCM) Aceria tosichella (Keifer) is the primary vector of wheat streak mosaic virus (WSMV), a sporadic and economically significant disease of wheat. Volunteer wheat in the wheat-fallow has been identified as the primary reservoir of the mite and virus and can perpetuate wheat streak mosaic reservoirs by sustaining the mite between spring and winter wheat crops. Replacing fallow with the incorporation of a non-host legume offers a possible control of volunteer wheat. A legume covercrop incorporated into the wheat-fallow was infested with varying densities of simulated volunteer wheat and examined for effects on the population dynamics of the WCM and the influence of WSMV on legume-wheat interactions in field and greenhouse trials. Significant treatment impacts were seen on mite populations in only 1 of 4 locations by years, that location was also the site with the overall greatest mite population. The one wheat and pea treatment combination in which mite populations showed significant increase in field trials occurred at the highest wheat-pea plant density. Environmental conditions were found to be directly influential on wheat curl mite populations and indirectly influential on the microenvironment in the canopy through mediation of the environment by wheat-pea treatments. Mite numbers were found to be strongly influenced by temperature and to a lesser extent by precipitation in the absence of peas. However, environmental influences changed in the presence of peas. Results obtained from the experiment indicate that the volunteer wheat densities studied in a pea crop do not adversely affect AWP biomass production at any wheat density in the field or in the greenhouse.

INFLUENCE OF A LEGUME COVERCROP ON VOLUNTEER

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WHEAT STREAK MOSAIC VIRUS

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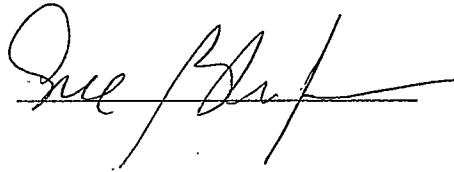MONTANA STATE UNIVERISTY-BOZEMAN
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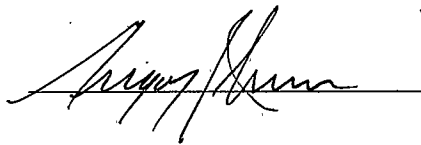
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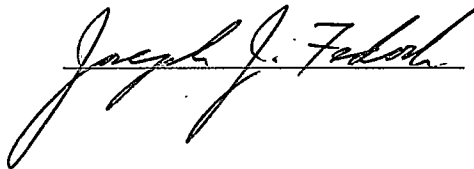
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TABLE OF CONTENTS

TABLE OF CONTENTS—CONTINUED

LIST OF TABLES

LIST OF TABLES—CONTINUED

LIST OF FIGURES

ABSTRACT

The wheat curl mite (WCM) *Aceria tosichella* (Keifer) is the primary vector of wheat streak mosaic virus (WSMV), a sporadic and economically significant disease of wheat. Volunteer wheat in the wheat-fallow has been identified as the primary reservoir of the mite and virus and can perpetuate wheat streak mosaic reservoirs by sustaining the mite between spring and winter wheat crops. Replacing fallow with the incorporation of a non-host legume offers a possible control of volunteer wheat. A legume covercrop incorporated into the wheat-fallow was infested with varying densities of simulated volunteer wheat and examined for effects on the population dynamics of the WCM and the influence of WSMV on legume-wheat interactions in field and greenhouse trials. Significant treatment impacts were seen on mite populations in only 1 of 4 locations by years, that location was also the site with the overall greatest mite population. The one wheat and pea treatment combination in which mite populations showed significant increase in field trials occurred at the highest wheat-pea plant density. Environmental conditions were found to be directly influential on wheat curl mite populations and indirectly influential on the microenvironment in the canopy through mediation of the environment by wheat-pea treatments. Mite numbers were found to be strongly influenced by temperature and to a lesser extent by precipitation in the absence of peas. However, environmental influences changed in the presence of peas. Results obtained from the experiment indicate that the volunteer wheat densities studied in a pea crop do not adversely affect AWP biomass production at any wheat density in the field or in the greenhouse.

INTRODUCTION

Wheat-summer fallow strip cropping is the most widespread dryland cropping system in the northern Great Plains. An estimated 6 million hectares are fallowed annually in the North American Great Plains region, stabilizing small grain production by conserving soil moisture and erosion in regions of sporadic or marginal rainfall. Weeds and volunteer plants from viable seed deposited during crop years can infest fallow areas whenever growing conditions are favorable. Weed management tactics are applied to fallowed strips to control weeds and volunteer grain. Methods of weed control in fallow strips include tillage and/or herbicides. There are few options for controlling seedling wheat plants in planted wheat fields.

The wheat curl mite (WCM), *Aceria tosichella* (K.) is a small mite, 150 to 250μ in length, belonging to the family Eriophyidae. The WCM was recognized as an economic pest of wheat (*Triticum aestivum*) in 1953 when it was determined to be the vector of wheat streak mosaic virus (WSM) (Slykhuis 1953).

WSM is a disease in wheat that occurs sporadically in North America, Eastern Europe and Russia (Slykhuis 1967); it was first identified in Montana in 1954 on winter wheat (Bamford et al 1996). A combination of WCM feeding and the WSM disease produce symptoms that include leaf chlorosis of varying intensity, leaf roll, necrosis, stunting and plant death (Slykhuis 1955). Although the WCM is endemic to the north central Great Plains, outbreaks of WSM are responsible for substantial economic losses.

In 1988, WSM caused a 13% wheat yield loss, an estimated $150 million loss in income, in Kansas (Sim and Willis 1988). During the last outbreak in Montana in 1993, WSM caused a $12.7 million dollar loss to winter wheat revenues in Montana (P. Brukner, personal comm.).

The WCM is an efficient vector for the WSM disease but can acquire WSM only during immature stages by feeding on infected plant material (Slykhuis 1965). The virus is transmitted transtadially, so once virus acquisition occurs, the mite can transmit the virus through the remainder of its life (Slykhuis 1965). WCM have multiple generations and under ideal conditions WCM can increase quickly requiring only 10 days to complete their life cycle (Slykhuis 1955). Adult WCM are dispersed passively by wind and some insects and can spread readily into adjacent fields (Gibson and Painter 1957). The persistence of the virus through the life of the mite combined with the mites small size and ability to rapidly reproduce and spread into adjacent wheat fields (Slykhuis et al. 1957, Slykhuis 1962), makes the WCM an efficient vector of the WSM disease.

Sampling programs for detecting WCM have not been developed because disease outbreaks are sporadic and the ability to detect an economic population is costly and time consuming due to the small size of the WCM. Detection of the WCM relies on WSM disease symptoms. However, symptoms are not always a reliable means for identification of WSM, as the symptoms will vary with time, temperature, soil moisture, soil fertility and wheat variety (Staples and Allington 1956).

Presently, management strategies directed toward controlling the WCM emphasize cultural methods that prevent the buildup of host material that favors WCM population growth. Control of the WCM is focused on the elimination of the "green

bridge", the continuum of green host material for the WCM and WSMV that allows the carryover of the mite from one crop to the next. Continuously available green host material can result from variable planting times, germination of volunteer wheat or from wheat that germinates from mature seed heads shattered by hail. Germination and growth of host plants in fallowed areas can provide a green bridge for WCM during the fallow rotation between winter wheat crops or between winter wheat-spring wheat crops to a new winter wheat crop. In addition, hail and other weather events that cause mature seed heads in wheat fields to break, drop to the ground and germinate can produce a flush of seedling wheat plants within a wheat field that can also be utilized by the WCM. Delaying winter wheat planting breaks the "green bridge" and avoids WCM infestation from spring planted crops to fall seeded winter wheat (Slykhuis 1955, Bamford et al. 1996). Pest management programs for the WCM have been limited because, (i) there are no sampling procedures for monitoring WCM and (ii) once disease symptoms are observed it is too late to control the WCM vector.

A survey of potential annual and perennial grass hosts in Montana found few resident grasses that can act as an alternative host for either the WCM or WSM or both (Brey 1998). However, resident grasses in Montana are not thought to play a significant role in WSM epidemiology because of poor host switching by the WCM between different host plants (Rosario and Sill 1965, Brey 1998). Volunteer wheat in the wheat fallow has been identified as the primary reservoir for the WCM and WSM and is considered the most significant factor in WSM epidemiology (Brey 1998).

Currently, few alternate crops are included in the dryland cereal cropping system. Diversifying the wheat-summer fallow strip cropping system offers several benefits,

including breaking insect and disease cycles, improving soil fertility and offering growers alternative enterprises for greater economic stability. Climatic constraints limit the selection of alternative crops that can be produced economically in our region. Research conducted at MSU has identified legumes adapted to our region, such as Austrian winter peas (*Pisum sativum* L.), that are compatible with the dryland cropping system in the north central Great Plains region and are capable of replacing summer fallow in the wheat-fallow system (J.R. Simms 1994).

Incorporation of alternative non-host crops into the wheat-fallow strip cropping system offers a possible cultural method for controlling WSM through plant competition, between host and non-host plants, and through non-host influence on WCM population dynamics. This study investigates the impact of incorporating a non-host covercrop into fallow ground on the population dynamics of the WCM and incidence of WSM. The objectives of the study were twofold, (i) investigate the impact of intercropping a legume with simulated populations of volunteer wheat on the population dynamics of the wheat curl mite *Aceria tosichella* (K.) and (ii) investigate how infection of wheat by WSM effects plant-plant interactions in a legume-wheat intercrop.

Life History of *Aceria tosichella* (K.)

The wheat curl mite was first described by Keifer (1936) as *Aceria tulipae* (K.)
collected from tulips in California. In 1970, Shevtchenko showed that the name *tulipae*
should only apply to mites developing on Liliaceae and described a new species *Aceria
tritici* for mites that utilize wheat as a host plant. However, in 1969 Keifer described an
identical *Aceria* species, *Aceria tosichella*, collected from wheat in Yugoslavia. Because
Aceria tosichella was published prior to *Aceria tritici*, the name *Aceria tosichella* takes
priority by the Rules of Zoological Nomenclature.

Members of the family Eriophyidae are minute, soft-bodied, cigar shaped mites
averaging 150 to 250μ in length and have two pair of legs located at the anterior end of
the body. The WCM can complete development in 6-7 days and averages 10 days from
egg hatch to cessation of egg lay (Slykhuis 1955). Reproduction is primarily
parthenogenetic and can begin as early as 7 days after egg hatch at 24°C to 27°C.
Females lay an average of 12 eggs that incubate for 3 days (Slykhuis 1955, Staples and
Allington 1956). *Aceria tosichella* has two nymphal instars. Each individual nymphal
stage lasts 1½ days with ¾ of a day for molting (Staples and Allington 1956). The
second nymphal stage ends in a resting period or "pseudopupa" during which the
genitalia of the female form and protrude through the body wall (Slykhuis 1962). Males
can occur but are rarely seen (Slykhuis 1962). *Aceria tosichella* (K.) transmits WSM
easily between healthy wheat hosts. Eggs of the WCM do not carry WSM (Slykhuis

1965). Nymphs can acquire the virus by feeding on infected plant material for thirty minutes or longer, while adults do not seem capable of acquiring the virus (Slykhuis 1965). However, the virus is transmitted transtadially and once a mite has acquired the virus it is infective for life.

Eriophyid mites rely on passive dispersal. WCM are primarily wind dispersed but can also be moved by birds, insects and other carriers or mechanically by distribution of infested plant material. Gibson and Painter (1957) considered WCM dispersal by aphids as a secondary means of WCM dispersal but felt it could be a significant factor in placing WCM directly onto volunteer wheat or other suitable hosts.

Eriophyids are an economically important family and damage plants by the formation of galls, blisters, bud swelling, rolled leaves, russeting and erineum (Keifer et al. 1982). Although WCM do cause direct damage to their host plants, they are important as a vector of wheat streak mosaic (WSM) and high plains virus (HPV). Symptoms of WCM infestation are often masked by WSM disease symptoms. Feeding by WCM on wheat causes the margin of the wheat leaves to roll inward, forming a tightly rolled tube that catches the tip of the next emerging leaf causing it to form a loop. Orlob (1966) found that WCM prefer to feed in tightly rolled leaves or in the leaf whorl. The tightly rolled leaf has higher humidity (Orlob 1966) and offers some protection from adverse environmental conditions and natural enemies.

WCM prefer to feed on the newest growth of the plant. Immature WCM feed parallel to the leaf in the adaxial groove between the leaf veins. Adult WCM either occupied the same position or lay perpendicular to the vein, bending down to feed in the adaxial groove (Orlob 1966). WCM feed on cells from both sides of the groove and on

cells located at the bottom of the groove. WCM penetrate epidermal cells by firmly attaching to the leaf surface with their terminal pads and contracting the rostra, forcing their stylets into the leaf tissue (Orlob 1966).

Strains of the WCM have been identified that were collected from and adapted to wheat (*T. aestivum*), western wheat grass (*Agropyron smithii*), onion (*Allium cepa*) (Rosario and Sill 1965) and corn (*Zea mays*) (Nault and Briones 1967). Rosario and Sill (1965) reported that WCM occurring naturally on wheat adapted with difficulty to *A. smithii* and onion but adapted easily to corn. Their research indicated that most individuals died rapidly when cross infecting from other grass hosts to wheat. A few WCM fed and survived for short periods but did not reproduce and a minority of WCM survived and reproduced with their progeny generally surviving longer.

A. tosichella feeds on and damages a variety of cultivated and resident perennial and annual grass plants. Historically, extensive surveys have been performed to evaluate the suitability of a variety of perennial and annual grass species as hosts for the WCM and WSM and their importance in WSM epidemiology. These surveys were based on the assumption that resident perennial and annual grasses played an important role in the epidemiology of WSM by influencing the density and distribution of the WCM population and by providing an oversummering bridge for the WCM. However, in contrast to previous survey results, research conducted at Montana State University by Brey (1998) has found few resident perennial grasses that are suitable hosts for the mite and virus. Grass species positive for either WSMV or WCM (Table 1), including resident grasses found positive previous to Brey (1998), and grasses that are negative (Table 2) are summarized. For a resident grass population to be an important alternate

host in WSM epidemiology, several requirements must be met. Alternate host grasses must (i) function as an oversummering bridge for WSM, (ii) support sufficient WCM for an epidemic to occur, (iii) occur in sufficient densities near a susceptible crop, (iv) emerge before wheat maturation and survive until fall emergence of wheat crops, (v) be suitable carrier of WSM and (vi) allow multiplication of the virus to occur. (Christian and Willis 1993).

Historically, perennial grasses were considered the primary host of the WCM because they could provide a continuum of living tissue to serve as a green bridge between crops. However, perennial grasses are not implicated in major epidemics (Slykhuis 1965). Perennial grass may be a good host for the WCM but will not support WSMV or will support the virus but not the WCM vector (Staples and Allington 1956, Christian and Willis 1993). Host quality must also be sufficient for successful WCM reproduction to contribute to an epidemic.

Cultivated wheat crops, volunteer wheat and other annual plants are the major hosts involved in the epidemiology of WSM outbreaks (Slykhuis 1965). Resident perennial and annual grasses are considered native reservoirs but are not thought to influence disease propagation (Slykhuis 1955). While small numbers of mites have been detected on grass species considered to be poor hosts, it is considered unlikely that such small numbers could establish a successful disease foci in either volunteer or winter wheat (Staples and Allington 1956). This is further supported by the findings of Brey (1998) who found no resident perennial or annual grasses other than cultivated grains that could play a significant role in WSM epidemiology in Montana (C. Brey, personal comm.).

Table 1. Annual and perennial grasses surveyed and found positive for WSMV and/or WCM.

	Scientific name	Common name	WSMV	WCM	Authority
Cultivated	*Avena sativa* (L.)	Oats	Yes	No	McKinney (1937), Slykhuis (1952)
	Hordeum vulgare L.	Barley	Yes	Yes	McKinney (1937), Slykhuis (1952), Sill (1953)
	Panicum miliaceum	Pearl millet	Yes	No	Sill and Agusiobo (1955)
	Panicum ramosum	Pearl millet	Yes		Sill and Agusiobo (1955)
	Secale cereale L.	Rye	Yes	Yes	Slykhuis (1952)
	Setaria italica (L.) Beauv.	Italian millet	Yes	Yes	Slykhuis (1952), Sill and Agusiobo (1955)
	Sorghum vulgare Pers.	Sorghum cultivars	Yes		Harvey and Seifers (1991)
	Triticum dicoccum Schrank.	Wheat	Yes	Yes	Slykhuis (1955)
	Tritticum durum Desf.	Wheat	Yes	Yes	Slykhuis (1955)
	Tritticum aestivum L. (spring types)	Spring wheat	Yes	Yes	Slykhuis (1955)
	Tritticum aestivem L. (winter types)	Winter wheat	Yes	Yes	Slykhuis (1955)
	Zea mays L.	Corn	Yes	Yes	Mckinney (1937), McKinney and Fellows (1951), Slykhuis (1952, 1955) Sill and Agusiobo (1955)
Annuals	*Aegilops crassa* Boiss.		Yes		McKinny (1937), McKinney and Fellows (1951)
	A. cylindrica Host	Jointed goatgrass	Yes		McKinney (1937), McKinney and Fellows (1951)
	A. ovata L.		Yes		McKinney (1937), McKinney and Fellows (1951)

	A. triuncialis L.	Barbed goatgrass	Yes		McKinney (1937), McKinney and Fellows (1951)
	A. ventricosa Tausch		Yes		McKinney (1937), McKinney and Fellows (1951)
	Bromus japonicus Thunb.	Japanese chess	Yes	No	McKinney (1937), McKinney and Fellows (1951), Slykhuis (1952), Brey (1998)
	B. secalinus L.	Cheat	Yes	No	Slykhuis (1952)
	B. tectorum L.	Downy chess	Yes	No	Slykhuis (1952), Sill and Connin (1953), Brey (1998)
	Digitaria ischaemum Schreb.	Smooth crabgrass	Yes	No	McKinney (1937), McKinney and Fellows (1951)
	D. sanguinalis (L.) Scop.	Crabgrass	Yes		Slykhuis (1952)
	Echinochloa crusgalli (L.) Beauv.	Barnyard grass	Yes	Yes	Slykhuis (1952), Sill and Connin (1955)
	Eragrostis cilianensis (All.) Lutati	Stinkgrass	Yes	Yes	Slykhuis (1952)
	Haynaldia villosa Schur.		Yes		McKinney (1937), McKinney and Fellows (1951)
	Panicum capillare L.	Ticklegrass	Yes	No	Slykhuis (1952)
	Phalaris paradoxa		Yes		McKinney (1937), McKinney and Fellows (1951)
	Setaria verticillata (L.) Beauv.	Bur bristlegrass	Yes	Yes	Slykhuis (1952)
	Setaria viridis (L.) Beauv.	Green foxtail	Yes	Yes	Slykhuis (1952), Sill and Connin (1953), McKinney (1937), McKinney and Fellows (1951)
Perennials	*A. cristatum* (L.) Gaertn.	Crested wheatgrass	Yes	No	Brey (1998)
	Agropyron lasianthum Boiss.		Yes		McKinney and Fellows (1951)
	A. trichophorum (Link) Richt.		Yes		McKinney and Fellows (1951)
	Bromus inermis Leyss.	Smooth brome	Yes	Yes	Brey (1998)
	Elymus canadensis L.	Canada wild rye	Yes		McKinney (1937), McKinney and Fellows (1951), Sill and

				Connin (1953)
E. condensatus Presl.	Giant wild rye	Yes		McKinney (1937), McKinney and Fellows (1951)
E. giganteus Vahl.		Yes		McKinney (1937), McKinney and Fellows (1951)
E. virginicus L.	Virginia wild rye	Yes		McKinney (1937), McKinney and Fellows (1951)
Eragrostis trichodes Nutt.	Sand lovegrass	Yes		McKinney (1937), McKinney and Fellows (1951), Sill and Connin (1953)
Poa bulboa L.	Bulbous bluegrass	Yes		McKinney (1937), McKinney and Fellows (1951)
P. compressa L.	Canadian bluegrass	Yes		McKinney (1937), McKinney and Fellows (1951)
P. pratense L	Kentucky bluegrass	Yes	Yes	Brey (1998)
Stipa Comata	Needle & Thread grass	Yes	No	Brey (1998)
S. robusta Scribn.	Sleepy grass	Yes		McKinney (1937), McKinney and Fellows (1951)
S. viridula		Yes	No	Brey (1998)

Table 2. Cultivated and weedy and resident perennial and annual grasses surveyed and found negative as hosts for WSMV.

	Scientific name	Common name	Authority
Cultivated	*Panicum glaucum*	Pearl millet	Sill and Agusiobo (1955)
	Saccharum officinarum L.	Sugar cane	Mckinney (1937), Sill and Agusiobo (1955)
	Sorghum vulgare Pers.	Sorghum	McKinney and Fellows (1951), Slykhuis (1952), Sill (1953), Sill and Agusiobo (1955)
Perennials	*Agropyron Cillare* (Trin) French.		Slykhuis (1952)
	A. cristatum (L.) Gaertn.	Crested wheatgrass	Slykhuis (1952),
	A. dasystachyum (Hook.) Scribn.	Thickspike wheatgrass	Slykhuis (1952)
	A. desertorum (Fisch.) Schult.	Desert wheatgrass	Slykhuis (1952)
	A. elongatum (Host.) Beauv.	Tall wheatgrass	Slykhuis (1952)
	A. inerme (Scribn. & Smith) Rydb.	Beardless wheatgrass	Slykhuis (1952)
	A. intermedium (Host.) Beauv.	Intermediate wheatgrass	Slykhuis (1952)
	A. junceum (L.) Beauv.		Slykhuis (1952)
	A. pertenue (C. A. Myer) Nevski		Slykhuis (1952)
	A. repens (L.) Beauv.	Quackgrass	Slykhuis (1952), Sill and Connin (1953)
	A. rigidum Beauv.		Slykhuis (1952)
	A. smithii Rydb.	Western wheatgrass	Sill and Connin (1953)
	A. trachycaulum (Link) Malte.	Slender wheatgrass	Slykhuis (1952)
	A. trichophorum (Link) Richt.	Stiffhair wheatgrass	Slykhuis (1952)
	Andropogon gerhardi Muhl.	Big bluestem	Sill and Connin (1953)

	A. scoparius Michx.	Little bluestem	Sill and Connin (1953)
	Bouteloa spp.	Grama grass	Sill and Connin (1953)
	Bromus inermis Leyss.	Smooth brome	Slykhuis (1952)
	Cenchrus paucilflorus Benth.	Sandbur	Sill and Connin (1953)
	Festuca rubra L.	Red fescue	Slykhuis (1952)
	Oryzopsis hymenoides (Roem& Schult.) Ricker	Indian ricegrass	McKinney (1937), McKinney and Fellows (1951)
	Panicum virgatum L.	Switchgrass	Sill and Connin (1953)
	Phalaris arundinacea L.	Reed Canarygrass	Slykhuis (1952)
	Phleum pratense L.	Timothy	Slykhuis (1952)
	Poa pratense L.	Kentucky bluegrass	Slykhuis (1952)
	P. stenantha Trin.		McKinney (1937), McKinney and Fellows (1951)
	Sorghastrum nutans (L.) Nash.	Indiangrass	Sill and Connin (1953)
	Sorghum halepense (L.) Pers.	Johnsongrass	Sill and Connin (1953)
	Sorghum vulgare Pers.	Sorghum	Sill (1955)
Annuals	*Avena fatua* L.	Wild oats	Slykhuis (1952)
	Eleusine indica (L.) Gaertn.	Goosegrass	Sill and Connin (1953)
	Hordeum jubatum L.	Wild barley	Slykhuis (1952)
	Setaria lutescens (Weigel) Hubb.	Yellow foxtail	Slykhuis (1952)

Abiotic factors influence the population dynamics of the WCM and play a role in WSM epidemiology. Slykhuis (1955) found a positive relationship between increasing relative humidities and WCM survivorship at 5° C, 15° C and 25° C. Staples and Allington (1956) suggest that the WCM may be wind dispersed during warm periods in the winter and that WCM dispersal could occur throughout the year but could find no significant correlation between temperature and WCM dispersal. However, Nault and Styer (1969) did find a significant relationship between temperature and WCM dispersal in research on eriophyid mite dispersal. Events such as rainfall and hail can also influence the population dynamics of the WCM. Hail can shatter mature seed heads prior to harvest and provide a flush of volunteer wheat that can act as a "green bridge" between infected spring and winter wheat crops and can also initiate new tillering on hailed wheat plants (Bamford et al. 1996). Both cases provide new plant growth for the establishment of a WCM population. Other factors such as plant morphology can also influence WCM population dynamics. Harvey and Martin (1980) found that highly pubescent wheat had higher infestations of viruliferous WCM than glabrous varieties. Increased pubescence may alter the microclimate of the phylloplane resulting in higher humidity near the leaf surface.

Because of multiple generations, the WCM is important in perpetuating large virus and vector reservoirs under favorable conditions within and between years and is capable of rapidly spreading WSM from adjacent infected sources (Slykhuis et al. 1957, Slykhuis 1962). Fall infected winter wheat provides an overwintering refuge for the WCM and WSMV. The following spring the mites multiply and disperse, infecting any

suitable hosts, especially less mature spring or volunteer wheat, perpetuating the mite and virus reservoirs in green bridge plant hosts for infection of fall sown crops (Slykhuis 1962). For WCM populations to reach outbreak levels, conditions that favor WCM population growth and dispersal need to be present. Specifically, the WCM must have (i) immature host plants or host tissue to infest (Slykhuis 1955), (ii) warm conditions that allow a population increase followed by cooler conditions that favor dispersal (Bamford et. al. 1996), and (iii) sufficient density of a host or alternate host to maintain a WCM population throughout the summer (Christian and Willis 1993).

Wheat Streak Mosaic Virus

Matthews (1991) formally defined a virus as a set of one or more nucleic acid template molecules, normally encased in a protective coat or coats of protein or lipoprotein, with the ability to organize its own replication only within suitable host cells. Virus replication is (i) dependent on the host's protein synthesizing machinery, (ii) uses host cell's resources, (iii) located within the host cell not separated by a lipoprotein bilayer membrane and (iv) continually giving rise to virus variants through various kinds of change in the viral nucleic acid (Matthews 1991). Virus symptoms in plants exhibit a variety of macroscopic symptoms that include: chlorotic lesions from loss of chlorophyll and other pigments, reduction in plant size, mosaic patterning of the early leaf stage, yellowing of leaf tissue, development of rings on leaf or fruit, death of plant tissue, organs or whole plant, developmental abnormalities, wilting, reduced nodulation and

genetic effects such as an increase in genetic mutation or genetic abnormalities (Matthews 1991). Other agents capable of causing virus-like symptoms include: toxins produced by arthropods, cellular parasites, genetic abnormalities, nutritional deficiencies, high temperatures, hormone damage, pesticides and air pollutants (Matthews 1991).

Viral diseases have cytological effects that impact cell structure or virus-induce structures in the cytoplasm. The cytopathological effect on cell structure varies but can impact cell nuclei, mitochondria, chloroplasts, cell walls, bacteroidal cells, myelinlike bodies or cause cell death (Matthews 1991). Viruses affect cell nuclei by inducing intracellular inclusions, influencing the function of the nucleolus or altering the physical form of the nucleus despite lack of visible virus reproduction. Virus-induced structures resulting from a viral infection include crystalline inclusions that consist mainly of virus particles that accumulate in an infected cell then form crystalline arrays or pinwheel inclusions. The formation of cylindrical inclusions in the cytoplasm of effected cells is a characteristic of potyviruses such as WSMV (Matthews 1991, Shukla et al. 1994).

Frequently, disease symptoms expressed by the plant reflect histological changes within the plant. Symptoms such as necrosis are variable in both timing of expression and in the tissues or organs it impacts and commonly occur in combination with other histological changes (Matthews 1991). Hypoplasia, the incomplete or arrested development of an organ or plant part and hyperplasia, an abnormal increase and enlargement in the number of cells in an organ or a tissue with consequent enlargement, are two histological changes that are common to diseased plants. Plants expressing mosaic symptoms usually show hypoplasia in the yellowed areas. Hypoplasia results in a

thinner lamina than in the green areas, decreased differentiation of the mesophyll cells causing a reduction in chloroplast formation and the reduction or absence of intercellular spaces (Matthews 1991). Hyperplasia can cause enlarged cells near the vein, cell division in differentiated cells, or the abnormal division of cambial cells. Enlarged cells near the vein are at least partly responsible for vein-clearing symptoms caused by some viruses (Matthews 1991).

The effects of viruses like WSMV on plant metabolism are extremely variable and are subject to a range of biotic and abiotic conditions. Plant stage, diurnal and seasonal variation and wound response all interact to provide a continuum of changing conditions that determines the effect a virus has on the host. Viral impact on a hosts metabolism include: changing plant membranes, alteration of carbohydrate synthesis or translocation or both, changes in respiration rate, reduction in photosynthetic activity, reduced transpiration, a decrease in auxin and gibberellin production, an increase in abscisic acid levels, an increase in one or both amides glutamine and asparagine, and a reduction in leaf pigments (Matthews 1991).

There are numerous vectors that transmit plant viruses. However, within the invertebrates there are species in only two phyla, the Nematoda and Arthropoda, who have many members that feed on terrestrial plants and have species that transmit viral diseases (Matthews 1991). Ninety-nine percent of all known vectors of plant viruses are insects (Harris 1981).

Only Hexapoda and Arachnida, of the Arthropoda, contain members that feed on plants. The important hexapod vectors of plant viruses are considered to be in the

Coleoptera, Thysanoptera and Homoptera (Harris 1981, Matthews 1991). Among the Arachnida two families within the Acari, Tetrarynchidae and Eriophyidae, have been found to vector viruses (Harris 1981, Matthews 1991).

Virus transmission from the invertebrate vector to a host can occur mechanically, by feeding or through injury to the plant. The piercing-sucking mouthparts of the homopterans makes them the most important vectors of plant viruses and allows viruses to be transmitted easily from diseased tissues or cells to healthy host plants (Matthews 1991). Eriophyid mites are known to transmit at least six viruses by puncturing the plant cells and sucking out the contents; transmission occurs when virus laden saliva is ejected during probing and feeding. *A. tosichella* is known to transmit three viruses simultaneously, wheat streak mosaic, high plains disease and wheat spot mosaic (Matthews 1991). There is no evidence of virus replication within mite vectors. However, WSMV is circulative based on finding WSMV particles in the midgut, body cavity and salivary glands, non-propagative within *Aceria tosichella* and is persistant for the lifetime of the mite (Matthews 1991).

Mosaic diseases of wheat were first observed in the United States in the spring of 1919 in fields of winter wheat near East St. Louis and Granite City, IL. When first diagnosed, the disease was mistakenly identified as take-all (McKinney 1937). Wheat streak mosaic virus (family Potyviridae), was first described in 1937 by McKinney (McKinney 1937). Slykhuis (1953) identified the wheat curl mite, *Aceria tosichella* (K.) as the primary vector for WSM in 1953. Although the WCM is the primary vector for WSM, some virus transmission did occur in experiments with leafhoppers (Slykhuis

1952) and aphids (McKinney 1937). WSM currently occurs in North America, Eastern Europe and Russia (Slykhuis 1967).

Abiotic factors such as temperature and biotic factors such as age of a host affect the incidence, severity and survival of WSMV in plant tissues at the time of inoculation. Temperature influences the duration of WSMV infectivity and incubation time. WSMV remains infective for up to 8 months at 4°C and -20°C and for approximately 1 month at room temperature (Sill 1953). Incubation period of WSMV within a host plant decreases with increasing temperatures. Sill and Fellows (1953) showed that average incubation time in wheat was 5 days with an ambient air temperature at 27.8°C, 7 days at 23.9°C, 9 days at 20°C, 15 days at 15.6°C and 23 days at 15.6°C with a soil temperature of 7.8°C.

Plant age influences the severity of the WSM disease. Slykhuis (1952) and observed that wheat plants infected at an early plant growth stage were affected more severely by the disease. Sill and Fellows (1953) reported that plants mechanically inoculated early in the two-leaf stage showed a lower incidence of infection but once infected were highly susceptible to damage by the virus and became severely stunted with strong mosaic symptoms. Plants inoculated at the third leaf stage to the 3-4 tiller stage were all inoculated successfully and always showed severe disease symptoms. However, infective WSMV was not found in wheat stubble or in the leaves of brown, fully dead plants (Sill 1953). This was confirmed by Slykhuis (1952) who showed that WSMV lost its infectivity quickly after the normal death of the host and found that infected green tissues stored under moist conditions lost infectivity more quickly than when air dried or desiccated. There is no evidence for WSM transmission by soil from

diseased wheat fields, by seed from diseased wheat, abrasive root contact, normal leaf contact in the greenhouse between diseased and healthy plants or through gentle handling (Slykhuis 1952).

Wheat that is heavily infected at early plant stages exhibits a variety of symptoms. Early symptoms usually begin with a faint green chlorotic mottling of the leaves that runs parallel to the leaf veins. The chlorotic mottling becomes more pronounced over time and eventually leads to complete necrosis. Later symptoms include visible plant stunting and extreme reduction in tiller height between tillers from the same plant, recumbent plant growth, complete or partial seed head sterility, poor kernel filling and in severe cases little or no seed head production in infected plants (Slykhuis 1952, Staples and Allington 1956, Atkinson and Grant 1967). Severely stunted plants may die without producing seed, severely impacting yield (Slykhuis 1965).

Cropping System

The most common dryland cropping system in the semi-arid Great Plains and Intermountain West farm region is an alternating wheat-summer fallow strip cropping system. This system relies on the fallow rotation to store soil moisture for a subsequent grain crop. However, fallowed areas must be managed for weeds to prevent depletion of soil moisture. Management relies on tillage or herbicides. Traditionally, this cropping system is dominated by cereal grain production. Alternative crops such as oil seed, or pulse crops are infrequently incorporated into the fallow rotation.

Legume crops, adapted to the Northern Great Plains, offer a way to diversify the

wheat summer-fallow strip cropping system and offer benefits in pest management, soil

fertility and soil structure (Risch et al. 1983, Reynolds et al. 1994). Legumes seeded into

a fallow strip can benefit growers by reducing insect damage, breaking insect and disease

pest cycles, improving soil fertility and reducing nitrogen applications. Additionally,

legumes offer flexibility in cropping system management to growers as forage or seed

crops or by use as a green manure through early incorporation. The flexibility of the

cropping system allows growers to make or change previous management decisions in

response to environmental and economic changes. Other positive responses that are

attributed to green manure or legume intercrops include increased yields of subsequent

cash crop (Oyer and Touchton 1990, Bauer et al. 1993, Torbert et al. 1996) and nitrogen

fixation by legumes in intercropped wheat and barley (Reynolds et al. 1994).

Legumes used as green manure crops can reduce the amount of applied chemical

nitrogen fertilizers by fixing atmospheric nitrogen into the soil. Rates of nitrogen fixation

and the amount of nitrogen provided by incorporating plant material into the soil vary by

legume species. Research by Mahler and Hemamda (1993) on the nitrogen fixation

ability of Austrian winter peas in Idaho (AWP) (*Pisum sativum* (L.) Poir) incorporated

three rates of semi-dried AWP material (1, 2 and 3 Mg ha^{-1}) into the soil. The

incorporated AWP material added 28-29 kg ha^{-1}, 56-58 kg ha^{-1} and 84-87 kg ha^{-1} of

nitrogen to the soil at 1, 2 and 3 Mg ha^{-1} respectively recovering an estimated 77% of

available nitrogen from the AWP material after incorporation. This compares favorably

with earlier research conducted by Mahler and Auld (1989) that evaluated three cropping

rotations. Their results showed incorporating AWP as a green manure resulted in a

nitrogen fertilizer equivalent of 94 kg ha^{-1} compared to 68 kg ha^{-1} left by the summer

fallow rotation. Although the summer fallow rotation is an economical rotation it

eventually depleted the finite organic matter component of the soil. Research conducted

by Reddy et al. (1994) and Sweeny and Moyer (1994) on legume cover crops also

indicates nitrogen availability from cover crops.

The organic matter added to the soil by a crop contributes to the physical structure

and fertility of the soil and helps prevent erosion. Legume cover crops or intercrops aid

in stabilizing erodible soil. Legumes intercropped with wheat or barley provide

increased ground cover that partially retards soil erosion and can physically improve the

soil characteristics, stabilizing erodible soils by increasing soil organic matter

(Biederbeck et al. 1993, Decker et al. 1994, Reynolds et al. 1994 Tanaka et al. 1997).

Soil moisture restricts the choice and management of cover crops. Cover crop

biomass production is strongly influenced by variable or sporadic precipitation (Tanaka

et al. 1997). Because water is a limiting factor, research has been done to evaluate water

use by annual legumes used as green manure in a dryland cropping system. Biederbeck

and Bouman (1994) evaluated water use of and residual soil moisture for black lentil,

Tangier flatpea, chickling vetch and feed pea cover crops. They reported that in wet

years legume cover crops significantly reduced downward water movement compared

with fallow and lowered the risk of nutrient leaching and increased salinization. In

addition, Biederbeck and Bouman (1994) report that legumes only used water from the

top 0.6 m of the soil. By tilling the legumes into the soil, water content in the top 0.6 m

increased until freeze up. They concluded that early incorporation of legumes for soil-water conservation was essential for replacing fallow with green manures.

Cover crops can aid in breaking disease and pest cycles. Risch et al. (1983) noted that by diversifying an agricultural habitat, the density of herbivore populations is frequently lowered. Vegetative heterogeneity that involves species mixtures and spatial arrangements within a field, has a major influence on insect population growth and results in islands or patches of favorable habitats for the insect (Power and Kareiva 1990). Because monophagous insect herbivores tend to be less abundant in plant communities of higher vegetative diversity, several hypotheses have been offered to explain why the presence of a non-host plant affects herbivore abundance. One proposed hypothesis is that insects are confused by the odors of non-host plants and are unable to find their host plants. This explanation is largely unsupported by evidence and is not applicable to many homopteran insects (Power and Kareiva 1990). A more accepted hypothesis is that lower numbers of monophagous herbivores in diverse habitats is a result of non-host plants affecting the emigration rates of herbivores rather than their colonization rates (Powers and Kareiva 1990). Additionally, a diversified agroecosystem would provide benefits over monocultures that include land conservation, reduced pesticide usage and decreasing pesticide resistance (Risch et al. 1983).

Lower numbers of monophagus herbivores in a diverse agricultural habitat should result in less damage to crop plants. Ampong-Nyarko et al. (1994) evaluated cowpea-sorghum intercrops on stem borer yield loss and reported a 28% loss to sorghum production in a monocrop compared to a 15% yield loss in intercropped sorghum and a

94% loss to a cow pea monocrop compared to a 51% loss when intercropped. Additionally, Riggin-Bucci and Gould (1997) showed that diamondback moth populations in toxic and nontoxic plant mixtures may decline even when populations in nontoxic monocrop fields are increasing.

The theory of managing plant diseases through agricultural diversification is similar to the theory used for arthropod pests. In a review of diseases under conservation tillage, Baily (1996) concluded that eliminating monocultures and diversifying crops in a rotation would lower the risk of diseases in cereal and oilseed crops. Yield loss in wheat from common root rot was 11% less in diverse rotations such as wheat-canola-spring wheat-lentil, spring wheat-pea-spring wheat-lentil, spring wheat-flax-winter wheat-peas, wheat-canola-canary seed-lentil than in a continuous wheat crop. Wheat loss to leaf spot infection was 28% greater in consecutive wheat crops than in rotations where wheat was not grown consecutively (Baily 1996). In experiments on aphid-vectored potyviruses in monocultures and polycultures of gamagrass spp., Piper et al. (1996) reported a decrease in the severity and incidence of disease on eastern gamagrass in two species mixtures with wildrye and two species mixtures with bundleflower and three species mixtures with bundleflower and wildrye. Research conducted by Ristaino et al. (1996), Akanda and Mundt (1997), and Colbach et al. (1997) also support reduced disease incidence through diversification of cropping systems.

Often there is a negative correlation between host density and disease incidence when infections result from a primary cycle and inoculum is limiting. The incidence of many aphid-vectored diseases is negatively correlated with host plant density. As host

density is increased, the number of infected plants increases at a slower rate than uninfected plants in the population, resulting in a lower proportion of infected plants (Mundt 1990).

Incorporation of annual plants, such as legumes, into the dryland wheat summer-fallow strip cropping system can be an important management strategy for insect and disease control. The primary WCM and WSM reservoir is volunteer wheat in the fallowed areas, annual and perennial grasses are not significant reservoirs in WSM epidemiology because of the lack of host cross infectivity by the WCM. Diversification of the fallow by incorporating a non-host of the WCM should decrease WCM populations and reduce the incidence of plant diseases, specifically WSM, while increasing soil fertility and soil structure. Incorporation of alternative crops into the wheat summer-fallow strip cropping system will offer growers a cropping system that can be flexibly managed for current economic and environmental conditions while reducing applications of chemical fertilizers such as nitrogen.

GREENHOUSE RESEARCH

Introduction

Diversifying the traditional wheat summer-fallow strip cropping system offers several benefits including breaking insect and disease cycles, improving soil fertility and greater economic stability by offering growers alternative enterprises. Although climatic constraints limit the selection of alternative crops that can be produced economically in our region, research conducted at MSU has identified legumes adapted to our region, such as Austrian winter peas (*Pisum sativum* L.) (AWP). Incorporation of a non-host legume, for both WCM and WSMV, into wheat fallow offers a potential cultural method for controlling WSM.

This study investigates WCM population dynamics and plant interactions using simulated volunteer wheat seeded into two different seeding rates of AWP and in wheat alone plots. The controlled conditions of the greenhouse should remove or minimize the influence of abiotic factors on WCM population dynamics and on wheat-pea interactions. Controlling inputs such as watering, temperature and fertilizer should allow the WCM population to develop and disperse under less variable conditions. The interaction between the wheat and peas under non-stressed greenhouse conditions was evaluated for

competition effects both in the presence and absence of WSM. Results obtained from the

greenhouse experiments will offer insight into larger scale field trials under conditions

more typical of the Northern Great Plains.

Materials and Methods

Greenhouse experiments were conducted at the Montana State University Plant

Growth Center, Bozeman Montana. Six boxes measuring 0.91 m by 3.04 m by 0.20 m

deep were divided into three 0.91 m by 0.91 m plots by using two 0.91 m sections of 5.1

cm by 15.24 cm board. Boxes were filled with 17.78 cm of soil consisting of a 60/40 mix

of sand and loam, allowing a 2.54 cm space at the top for watering. Soil was fertilized

with 15% N / 30%P_2O_5 / 15% K_2O fertilizer prior to planting and as needed during the

experiment. Greenhouse temperature was maintained at 23.8°C during the day and 20°C

to 21.1°C at night throughout the experiment.

A split plot factorial design was used with WCM infested and non-infested

treatments as main plots. Subplot treatment combinations were randomly assigned within

the main plots and consisted of three seeding rates (3, 14, 22 kg/ha) of spring wheat

variety 'Fortuna', and three seeding rates (0, 45, 90 kg/ha) of AWP arranged in a 3 by 3

factorial design. Treatments were replicated three consecutive times. Wheat rates were

chosen to simulate low, medium and high populations of volunteer wheat. AWP

densities were seeded at one-half and full recommended seeding rates to simulate poor

and good stands of AWP, respectively. Main plots were designed to measure the effect

of plant competition and WCM infestation on biomass. Subplots within main plot treatments were grouped together to prevent WCM infestation of uninfested plots. A 3.96 m long 3.8 m high barrier constructed out of opaque 6 mil plastic (Carlisle Plastics, Inc., Minneapolis, MN) divided the greenhouse separating the main plots. The material of the barrier was later changed to a clear 6 mil plastic to allow more light to pass through to plots close to the barrier. Subplots were planted by hand at 5.08 cm row spacings in 0.86 m long rows.

To reduce the impact of aphids and thrips in the plots and to eliminate WCM in the uninfested plots, a variety of chemical and biological control measures were used. Acephate (Valent, Walnut Creek, CA), aldicarb (Rhone-Poulenc, Research Triangle Park, NC) and primicarb (Zeneca Ag Products, Des Moines, IA) were used as needed to reduce the interference by other arthropods. Foliar applications were applied using a hand sprayer. Minute pirate bugs (Orius spp.) and predatory mites (*Phytoseiulus persimilis*) were used to control thrips infestations. Lady bird beetles (*Hippodamia convergens*) were released to control periodic Russian wheat aphid (*Diuraphis noxia*) infestations.

Evaluation of primicarb and acephate indicate that at the applied rates no WCM mortality was detected. Acephate can act as a herbicide on some plants and did negatively effect the AWP, causing treated leaves on some plants to have brown, patchy necrotic areas and become dry and brittle. Plants showing these symptoms usually died despite repeated applications with fertilizer.

WCM Infestation

Infested main plots were inoculated at Zadok stage 23 (main shoot with three tillers at the second leaf stage) (Zadoks et al. 1974) with viruliferous WCM from a colony maintained by the Department of Entomology at Montana State University. Prior to inoculation, mean number of mites per gram of plant material was determined by randomly selecting and weighing ten WCM infested spring wheat plants and counting the number of WCM present. WCM infested leaf material used for inoculation was cut into fragments approximately 2 cm in length, weighed, and then divided into 2 to 3 gram units containing approximately 168 WSM viruliferous mites. Each unit was individually packaged in a resealable plastic bag. One package of infested spring wheat leaf material was used to inoculate each subplot within the infested main plot. Infested plant material was sprinkled onto spring wheat in the individual plots. Because a successful infestation was vital, plots were observed for WSM symptoms after 10 days. If no symptoms were observed, plots were reinoculated with an additional gram of infested plant material.

Plant Stand and Biomass

Wheat and pea stand densities were assessed on 27 October and 6 November, 1995 for replication 1, 8 and 16 April 1996 for replication 2 and 4 and 18 March, 1997 for replication 3 by counting the total number of wheat and AWP plants present in each subplot. Cereal grain development stage was determined at this time using the Zadok scale.

Plant samples were taken on 13, 20 and 30 November and 6 December, 1995 for replication 1, 28 May and 5 June, 1996 for replication 2 and 18 April and 15 May, 1997 for replication 3. Samples were collected for biomass by randomly throwing a $0.1m^2$ hoop and clipping all plant material in the defined area at the soil surface. Plant biomass was separated by species, placed into paper bags and dried at 48°C for 14 days. Dry weights were recorded after drying.

WCM Population

WCM were sampled at 5 day intervals beginning 20 October 1995 for replication 1, 18 April 1996 for replication 2 and 28 March 1997 for replication 3. WCM sampling consisted of randomly selecting one fifth of the total number of wheat plants determined by the seeding density and removing the last fully expanded leaf below the ligule. Samples were placed into plastic bags and held in a freezer until examination. Leaves were visually inspected for WCM with the aid of a 50x Zeiss dissecting microscope (Carl Zeiss Inc., Thornwood, NY). Mean number of mites per leaf and percentage of leaves infected were determined.

Data Analysis

Mean number of mites, percent infestation and biomass were subjected to an analysis of variance using Proc GLM in SAS (SAS Institute 1996). Linear regressions

were performed on the dependent variables: mean number of mites, percent infestation and biomass, using Sigma Plot (SPSS 1997).

Results and Discussion

WCM

There was a significant wheat main effect for mean number of mites per leaf (F = 6.12; df = 2; P > 0.01) and percent infestation of sample (F = 11.21; df = 2; P > 0.001) (Table 3). The interaction between the wheat and pea plant densities was significant for percent infestation of sample (F = 3.70; df = 4; P > 0.03), but there was no interaction between these factors for mean number of mites per leaf.

Table 3. Analysis of variance for mean percent sample infestation and mean number of mites per leaf in the greenhouse. $\alpha = 0.05$.

	Greenhouse			
	Percent infestation		Mean no. mites / leaf	
Source of variation	F-test	p > F	F-test	p > F
Model	10.80	0.0001	9.18	0.0001
R^2		0.87		0.85
Wheat	11.21	0.0009	6.12	0.011
Pea	0.90	0.43	0.29	0.75
Wheat*Pea	3.70	0.03	0.53	0.72

Percent infestation. The percentage of plants infested increased over the duration of the sampling period in all treatment combinations (Fig. 1A-C). The change in percent infestation by WCM increased at similar rates in the zero and low-density pea plots for all densities of simulated volunteer wheat (Figs. 1A and 1B). However, at the high seeding density of peas the rate of increase of percent-infested plants at the high wheat density (slope = 0.10) was lower compared with the low (slope = 0.18) and medium (slope = 0.15) densities of wheat. The high wheat and pea density plots had the greatest total plant density and may have interfered with the WCM ability to disperse under greenhouse conditions resulting in a lower rate of increase in the percent plants infested by the WCM. Summarizing across sample dates, percent infested plants generally decreased with increasing densities of the wheat host (Table 4). The percent infestation at the 3 kg/ha wheat and 45kg/ha AWP seeding rates was significantly different than the percent infestation at all pea densities at the high rate of simulated volunteer wheat (Table 4).

Wheat density was a significant factor in percent infestation. The rate of percent infestation increased and tended to be greatest at the lower wheat densities, decreasing with increasing densities of wheat (Table 4). Mite dispersal, represented by percent infestation, was favored at the lowest density of volunteer wheat (Table 4).
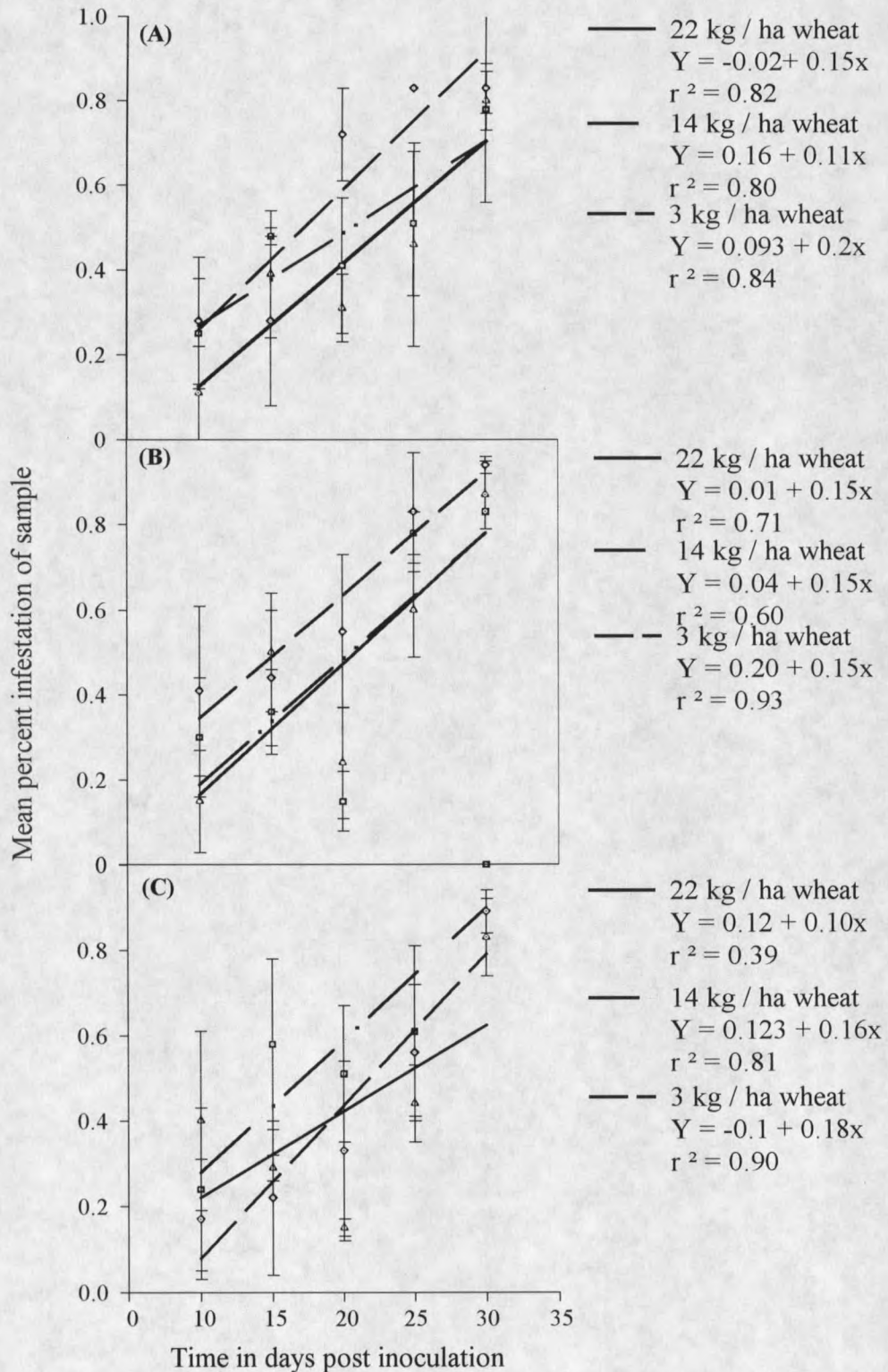
The WCM use wind to passively disperse and are unable to actively direct their movement to a suitable host plant. Population pressure (Power and Kareiva 1990), host quality (Perring et al. 1986, Margolies 1987) and abiotic factors such as wind and temperature (Staples and Allington 1956, Nault and Styer 1969) can all influence

Table 4. Mean separation of wheat-pea combinations for percent sample infestation in the greenhouse.

Greenhouse

Wheat rate	Pea rate	Percent infestation	
22	90	43.0	C
22	45	49.0	BC
22	0	48.0	BC
14	90	65.0	AB
14	45	54.0	ABC
14	0	56.0	ABC
3	90	51.0	ABC
3	45	69.0	A
3	0	63.0	ABC
$\alpha = 0.05$	**Std Err**	0.04	

*Means with the same letter are not significant.

Figure 1. Mean percent plant infestation from inoculation through time
for 3, 14 and 22 kg/ha at (A) 0 kg/ha, (B) 45 kg/ha and
(C) 90 kg/ha AWP. Greenhouse 1995-1997.

(A)

22 kg / ha wheat
$Y = -0.02 + 0.15x$
$r^2 = 0.82$

14 kg / ha wheat
$Y = 0.16 + 0.11x$
$r^2 = 0.80$

3 kg / ha wheat
$Y = 0.093 + 0.2x$
$r^2 = 0.84$

(B)

22 kg / ha wheat
$Y = 0.01 + 0.15x$
$r^2 = 0.71$

14 kg / ha wheat
$Y = 0.04 + 0.15x$
$r^2 = 0.60$

3 kg / ha wheat
$Y = 0.20 + 0.15x$
$r^2 = 0.93$

(C)

22 kg / ha wheat
$Y = 0.12 + 0.10x$
$r^2 = 0.39$

14 kg / ha wheat
$Y = 0.123 + 0.16x$
$r^2 = 0.81$

3 kg / ha wheat
$Y = -0.1 + 0.18x$
$r^2 = 0.90$

Mean percent infestation of sample

Time in days post inoculation

dispersal behavior in small arthropods, like the WCM. By controlling inputs such as temperature, water and fertilizer, a favorable greenhouse environment is maintained for both the mite and the wheat host. Mite dispersal in the greenhouse could be elicited by population pressure, decreased host quality resulting from maturity or disease, or through an interaction between plant maturity and population pressure. Because the dispersal reflected by the percent infested plants was relatively constant, mite dispersal in the greenhouse may be a good estimate of natural rates of emigration caused by population pressure in the absence of variable abiotic factors. Under more realistic conditions found in the field, mite dispersal is highly influenced by the interaction between abiotic factors, plant stress and plant maturity (Perring et al. 1986). In the absence of interactions resulting from variable abiotic conditions, it is not unreasonable to assume that the factors influencing WCM dispersal are primarily WCM density dependent. Air currents used in dispersal come from the natural movement of air provided by the ventilation system and were not subject to the same type of variation found in the field. This allows for stable dispersal through the system. WCM were able to locate wheat host plants and were able to colonize them effectively as indicated by the similar slopes between the percent infestation and time with increasing densities of non-host AWP. Numbers of dispersing mites may have been sufficient to overcome the interference provided by the presence of a non-host. While percent infested plants were seemingly unaffected by increasing densities of non-host, the lower rate of increase of percent infestation seen at the 22 kg/ha wheat rate at the high density of AWP (Fig. 1C) may indicate that there is a density of plants that can interfere with the WCM ability to disperse.

<u>WCM population</u>. Wheat density is a significant factor influencing the mean number of mites (F = 6.12; df = 2; P < 0.01). Mean number of mites per leaf at the 3 kg/ha seeding rate was significantly different from the 22 kg/ha wheat seeding density (Table 5). The rate of increase for mean numbers of mites during the sampling period tended to be higher in the lower wheat densities, indicated by the higher slope of the regression of mite population on time, decreasing consistently with increasing densities of simulated volunteer wheat (Figs. 2A-C and 3). However, as the density of volunteer wheat increases the per plant population of WCM decreases. Examining the effect that both wheat and pea densities together had on mite populations indicates that the strong effect that wheat density had on mite populations (Fig. 3). One possible explanation for lower populations of WCM with increasing densities of wheat is a combination of decreased susceptibility to both the WCM and WSM as the plant matures and plant tillering that provides new material at a rate that exceeds the WCM ability to colonize (Power and Kareiva 1990). However, it is more likely that greenhouse conditions favorable at the low wheat densities become less favorable for WCM populations as wheat density increases. In addition, by decreasing plant stress and maintaining factors such as temperature that are influential to WCM population development, higher populations of mites can be maintained on individual plants at all planting densities as seen by higher mite numbers in the greenhouse than in the field.