APHID AND DROUGHT STRESSES IN SMALL GRAINS: TRITROPHIC INTERACTIONS WITH APHID PARASITOIDS AND PLANT RESISTANCE

By

RUSSELL KENNETH CAMPBELL

Bachelor of Science
Oklahoma State University
Stillwater, Oklahoma
1977

Master of Science
Oklahoma State University
Stillwater, Oklahoma
1987

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Thesis Approved:

R D Eikenbary
Thesis Adviser

John R Sauer

David K. Reed

James A. Webster

Paul E. Richardson

Thomas C. Collins
Dean of the Graduate College

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PART I

SIGNIFICANCE AND REVIEW OF THE LITERATURE

SIGNIFICANCE

The grain production system in the United States is at a critical juncture with respect to its profitability. Increasing costs of inputs to the system coupled with declining real prices for grain have resulted in very small or negative profit margins. Small grains are often subject to periodic droughts and are also often infested by two important yield limiting aphids: the Russian wheat aphid, (RWA), Diuraphis noxia (Mordvilko), and the greenbug, (GB), Schizaphis graminum (Rondani).

The Great Plains is the most important region for production of high quality bread wheat, durum wheat, and barley in the United States. Bread wheat is extremely important for foreign export and balance of trade considerations as well as domestic use. Wheat and barley are also extremely important for the provision of livestock forage and feeds. Hence, any limitation of the productive capabilities for these grains may have serious repercussions not only for agricultural production of grains and meat but also for national well-being and economic security. Variations in annual precipitation and its unpredictability make dry-land grain production inherently uncertain. Only a relatively small percentage of the current United States grain production is aided by use of irrigation. Serious ongoing depletion of the massive Ogallala aquifer, which underlies much of the central and southern Great Plains, is continuing to reduce irrigation as a crop management option in some of the drier areas.

Drought and grain aphids often occur together or sequentially during the growing season. The two most economically important cereal aphids, the GB and the RWA, both cause serious yield reductions to both wheat and barley, and are especially devastating when they occur in combination. A recent economic analysis of RWA damage is instructive (Hein et al. 1990). Total losses due to the RWA in the U. S. since its detection in 1986 through 1989 were over $250 million. Losses due to GB solely in Oklahoma exceeded $80 million in the outbreak year of 1976 (USDA 1977). Field observations have indicated that aphid damage is greatly amplified when drought also occurs as a stress factor. It appears that both aphids are capable of preventing grains from adapting to dry conditions. Past approaches to aphid management have relied heavily upon insecticidal control measures. While this has been largely sufficient for GB control, the need for multiple applications or the use of expensive systemics for RWA control, when combined with the marginal profit margins for grain production, will require either alternative control methodologies or a cessation of grain production.

In the past, resistant varieties have been developed for GB management. However, this aphid has remained a problem because of its capacity to overcome the resistance sources by developing new biotypes. While recent work has uncovered RWA resistance sources in barley (Webster 1989) and wheat (Quick 1989), evidence suggests that the RWA exhibits substantial genetic variation which may allow it to also overcome resistant cultivars unless additional steps are taken to slow or prevent its adaptation (Puterka et al. 1992). Plant influences on aphid fecundity and host preference could play paramount roles in new biotype development. These plant influences on aphid adaptability may be moderated by parasitoid action. Consequently, a tritrophic approach to aphid management, in which plant resistance and biological control are used in harmonious conjunction, may be able to slow resistance breakdown. Additional benefits of such management would be derived from a reduction in insecticide usage and include profit enhancement for grain producers, limitation of aphid insecticide resistance development and reductions in non-point source pollution (runoff and groundwater contamination).

LITERATURE REVIEW

The Russian wheat aphid is a relatively new aphid invader to North America (Stoetzel 1987) that is indigenous to the Middle East and southern Russia (Hewitt et al. 1984). The RWA remained a rather obscure pest in its native range but became a very serious pest of wheat, barley, and triticale in the Republic of South Africa after its introduction in 1978 (Walters 1984). Wheat yield losses of 35 - 60% were experienced in South African field tests (du Toit and Walters 1984). RWA infestations were found in Mexico in 1980 (Gilchrist 1984) and then verified in the United States near Muleshoe, Texas in 1986 (Stoetzel 1987). Since then, the RWA has rapidly expanded its range throughout the major grain production regions of the U.S. and Canada. It is now found in seventeen states and three Canadian provinces (Hein et al. 1990). Major pest status of the RWA is generally limited to semi-arid regions since the aphid in North America apparently prefers dry environmental conditions (Webster 1990). The RWA causes heavily infested plants to exhibit striking damage symptoms, two of which are of particular importance. These two are its habit of causing plants to become prostrate and its ability to prevent the normal unrolling and expansion of leaves (Webster et al. 1987). Such unrolled leaves may then serve as refugia for the aphid colonies, and these may then partially protect them from attack by beneficial aphid parasitoids or the effects of contact insecticides.

The greenbug has long been considered one of the most injurious insect pests attacking grains in the United States. This aphid possesses a wide host range (Pettersson 1971, Michels 1986), but in recent years it has been expanding its adaptive range to colonize both new host species such as grain sorghum (Harvey and Hackerott 1969), Canada bluegrass (Kindler and Spomer 1986), and corn (Michels et al. 1987) as well as formerly resistant wheat lines developed in germplasm enhancement programs. A number of GB biotypes have been defined based on their ability to differentially damage previously reported GB resistance sources in wheat, sorghum, oats, rye, and barley (Puterka and Peters 1988, Puterka et al. 1988). The most agronomically important and prevalent greenbug biotypes in the field are C (GBC) and E (GBE) (Bush et al. 1987, Kerns et al. 1987).

The low profit margin potential for grain production in the U. S. has long encouraged the development of alternative control methodologies for dealing with GB infestations. However, with the new concerns occasioned by the recent RWA invasion, particularly the aphid's rolled leaf niche that requires the use of much more expensive systemic insecticides to achieve chemical control, efforts have been redoubled to find effective plant resistance sources and to import effective parasitoids of the aphids. An initial survey for RWA resistance sources did not uncover any suitable sources in wheat or barley comparable to those available for certain GB biotypes (Webster et al. 1987). A recent study has identified some promising resistance sources in wheat to a U. S. collected RWA population (Harvey and Martin 1990). Webster et al. (1991) screened 524 barley lines from areas of the world where the RWA is believed to be indigenous. They found at least six of these lines to exhibit significant RWA resistance. Twenty-one triticale lines were screened for resistance to both GB and RWA (Frank et al. 1989). Of these, five appeared to hold some potential for use in future wheat breeding programs as sources of resistance to one or both aphids. A more extensive study screened 731 triticale lines and uncovered seven that exhibited varying degrees of RWA resistance (Webster 1990). Du Toit (1987, 1988) initially identified three sources of resistance to RWA in wheat using RWA collected in South Africa and indeed, preliminary results indicated that wheat varieties possessing the 'Amigo' gene for GBC resistance exhibited some antibiosis to South African RWA (Butts and Pakendorf 1984). However, Webster et al. (1987) found that although fewer nymphs of RWA were produced on 'TAM 107' wheat (which incorporates the 'Amigo' gene) the differences were not significant compared to other wheat lines tested using a U. S. RWA population. This may imply biotypic variation between the U. S. and South African populations, and indeed recent work has reported differences among a worldwide collection of geographically distinct RWA populations (Puterka et al. 1992). Cuticular hydrocarbon compositions of RWA have also been shown to vary between different geographic collections (Bergman et al. 1990).

The recent RWA invasion has spurred increased efforts to upgrade and improve biological control through the use of aphid parasitoids. The parasitoid <u>Lysiphlebus</u> <u>testaceipes</u> (Cresson) is the most abundant and recurrent natural enemy of the GB in the U. S. (Jackson et al. 1970, Archer et al. 1974). Although L. testaceipes has often been observed having devastating effects on GB populations at outbreak levels and it has been shown to complement host plant resistance in the field (Hamilton et al. 1982), its buildup often comes too late to prevent significant plant damage. L. testaceipes can parasitize RWA in the field (Morrison 1988), yet early laboratory studies indicated that it greatly preferred the GB (Gilstrap and McKinnon 1988). However, field observations in the spring of 1990 found this parasitoid readily parasitizing RWA in Oklahoma, indicating that it had apparently adapted its host range to exploit RWA populations (R. K. Campbell, Okla. State Univ., unpublished). Since early evidence had indicated that L. testaceipes was relatively incapable of attacking RWA, an extensive effort has been undertaken to discover and import candidate biological control parasitoids for control of RWA. Most of these imported parasitoids are also good candidates for control of the GB. One of the largest groups of hymenopterous parasitoids to be imported include members of the Aphidiinae. This subfamily includes members closely related to L. testaceipes. Among the aphidiine species imported into the U. S. for RWA control in recent years are Diaeretiella rapae McIntosh, Aphidius matricariae Haliday, A. rhopalosiphi De Spain, A. uzbekistanicus Luzhetzki, A. ervi Haliday, and A. picipes (Nees) (Gilstrap 1990). D. rapae may be the most promising candidate for establishment and aphid control capability in the southern Great Plains. *A. matricariae*, *A. pascuorum* Marshall, *A. rhopalosiphi*, and *A. uzbekistanicus* were previously imported for GB control but establishment was not attained (Campbell et al. 1990a). The current strategy is to achieve establishment of one or more of the imported species somewhere in the U. S. with the hope that this will complement existing native species and result in enhanced natural biological control. This is congruent with classical biological control theory since the RWA is not a serious outbreak pest in its native range and is presumably at least partially held in check by some of these parasitoids which are being collected from that range. Unfortunately, as van Emden (1988) concludes "The literature is generally not encouraging about the value of indigenous natural enemies for the control of aphids." This is most often attributed to two factors, as Carver (1989) concludes: "Aphids are poor prospects for biological control because their high reproductive capacities and physiological activity at relatively low temperatures give them an unsurmountable advantage over natural enemies." I feel, however, that the lack of major pest status for RWA in its native range provides direct evidence for the efficacy of biological control when combined with plants expressing some resistance to the aphids. A 'critical lag period' may exist between aphid colonization of a plant and a parasitoid's discovery of and foraging on the plant. Consequently, this lag period may be a major determinant in the subsequent outcome of the aphid - parasitoid interaction as well as the extent of plant damage. Employment of plant resistance could serve to limit aphid buildup during this lag period thus improving the prospects for limiting plant damage by natural enemies.

Host plant resistance and biological control are often considered compatible pest management strategies (Bergman and Tingey 1979, Boethel and Eikenbary 1986). When both control methodologies are used concurrently, unrelated mortality effects are applied, which may reduce the rate of genetic adaptation in the pest population to selection pressures imposed by resistant germplasms, thus possibly slowing the development of new pest biotypes. Furthermore, even low levels of plant resistance can diminish the intrinsic rate of increase of a pest population thereby providing an advantage to natural enemies (van Emden 1966, Starks and Berry 1976). Some twenty-five years ago, van Emden and Wearing (1965) developed a simple model from which they proposed that the reduced rate of increase of insects such as aphids on partially resistant varieties should result in a magnification of the plant resistance in the presence of natural enemies. The prediction of van Emden and Wearing (1965) was experimentally validated by Starks et al. (1972) using GB and _L_. _testaceipes_ on resistant and susceptible varieties of barley. Schuster and Starks (1975) found that the response of _L_. _testaceipes_ was improved on a resistant variety of oats over a susceptible one. Salto et al. (1983) found no differences in the parasitization of GB on resistant and susceptible oats. Kuo (1986) concluded that oat resistance against cereal aphids and the effect of an aphid parasitoid appear complementary in reducing aphid populations but emphasized the importance of considering the effect on parasitoid fecundity and sex ratios. Parasitoid performance may be detrimentally altered by the host plant of the pest insect, especially if resistance is conferred by significant chemical antibiosis. Although different species of host plants can produce the greatest range in responses, cultivars of the same species can also differentially affect parasitoid success (de Ponti 1980). Auclair (1989) has concluded that resistance breeding is most often done without knowing the underlying basic nature of resistance and that such knowledge is not a prerequisite for the production of resistant cultivars. Prey confined to resistant plants quite often experience reduced growth rates and achieve smaller adult body size which can greatly reduce the nutritional quality and/or quantity of the prey for a parasitoid. Such prey also tend to have greater developmental times, increased mortalities, and decreased fecundities. Nutritionally inadequate diets have been shown to detrimentally alter the development, fecundity, and longevity of the aphid parasitoid _Aphelinus asychis_ Walker (Zohdy 1976). In addition to such nutritional influences, toxic compounds found in resistant cultivars expressing antibiosis can be passed through the trophic chain and affect parasitoids (Duffey et al. 1986). For example, fewer, smaller mummies of D. rapae that had decreased development rates were found when the parasitoid attacked RWA reared on an antibiotic variety of triticale (Reed et al. 1991). Phenolic compounds (Dreyer and Jones 1981), hydroxamic acids (Argandoña et al. 1981), and indole alkaloids (Corcuera 1984) have been implicated as antibiotic resistance factors against aphids in several small grain cultivars.

Recent research compared the effects of antibiotic resistance in barley ('Post') and a susceptible variety ('Wintermalt') on L. testaceipes using GBE as the aphid host (Campbell et al. 1990b). Parameters measured included parasitization success (% of females producing any mummies at all), days to the formation of the first mummy, mummy formation period, maximum number of mummies formed by a female in one day, the day number on which this occurred, and the mean total mummies produced per female. All parameters were influenced detrimentally by the antibiotic variety. Clearly, the concomitant use of both host plant resistance and biological control to reduce aphid losses in grains will require careful study of possible tritrophic interactions.

In addition to aphids, periodic drought can significantly limit grain production in the central and southern plains states. The relationship of moisture to plant health is well studied in a wide range of plants and has been documented in several comprehensive reviews (Hsiao 1973, Begg and Turner 1976, and Levitt 1980). More specifically, the effects of drought have been studied with small grain crops (Day et al. 1981, Quarrie 1980, Andjei and Kirkham 1980, and Keim and Kronstad 1980). Strategies for drought resistance differ among wheat cultivars (Keim and Kronstad 1980). Specifically, certain cultivars are able to avoid drought stress by adjusting osmotically and thereby maintaining a higher plant water status while other cultivars are inherently more tolerant of high internal moisture stress and can maintain a larger number of tillers through development to harvest. Considerable evidence exists to suggest that sap feeding herbivores such as aphids are influenced by their host plants' water status. However, the influence of the moisture-stressed plant may be favorable for the aphid, increasing its survival and reproduction, or it may be detrimental. Aphid and plant responses that have been reported vary. Kennedy et al. (1950) and Taylor (1955) offered evidence that drought-induced senescence favored larger populations of the green peach aphid, <u>Myzus persicae</u> (Sulzer). This phenomenon may be explained by the aphid's reproductive rate increasing in response to a rise in the nutritional value of the phloem available to aphids (Mittler 1958, Kennedy et al. 1958). Conversely, evidence exists that suggests decreased plant moisture may reduce the amount of aphid feeding and reproduction. Kennedy et al. (1958) suggested that lower reproductive rates of the black bean aphid, *Aphis fabae* (Scopoli), on water stressed plants resulted from a reduction in available phloem sap caused by either reduced turgor pressure (thought to be a mechanism involved in aphid feeding) or by increased sap viscosity. Both McMurtry (1962) and Kindler and Staples (1970) found no relationship between spotted alfalfa aphid, *Therioaphis maculata* (Buckton), survival or reproduction relative to soil moisture. Wearing and van Emden (1967) found that *A. fabae* reproduction was unaffected by water-stressed broad bean, *Vicia fabae* (L.), although cabbage aphid, *Brevicoryne brassicae* (L.), reproductive rates declined with increasing water stress in brussels sprouts, *Brassica oleracea gemmifera* Schulz. Moreover, reproductive rates of *M. persicae* on water stressed brussels sprouts were reduced while reproductive rates were highest at intermediate moisture levels. A few studies have been conducted to uncover interactions of grain aphids and drought stressed grains. Wheat infested with GBC and stressed with polyethylene glycol (PEG) reduced aphid fecundity and longevity when the plants' water status was reduced below a critical moisture level (Sumner et al. 1983). Subsequent studies were conducted to analyze the response of GBC to controlled levels of drought stress on resistant and susceptible wheat using PEG induced stress (Sumner et al. 1986a). The GBC resistant wheat selection 'OK 80268' (with the Amigo gene for resistance) and the GBC susceptible wheat cultivar 'Sturdy' were used. Results showed that GB longevity was not altered by the host plant but was significantly lowered by decreased water potentials (≤ -0.3 MPa). Fecundity, however, was dependent on the host plant, being significantly reduced on the resistant cultivar. Drought stress reduced GB fecundity on 'Sturdy' to levels equal to or lower than non-stressed 'OK 80268'. Drought stressed 'OK 80268' significantly depressed fecundity as well. Similar studies with the corn leaf aphid, Rhopalosiphum maidis (Fitch), showed that fecundity, longevity and reproductive period of the aphid declined linearly with increasing water stress levels (Sumner et al. 1986b). GB reproduction was similarly reduced on water stressed field grown grain sorghum (Michels and Undersander 1986). Dorschner et al. (1986) found that GB density (number of GB per mg shoot dry weight) was greater on drought-stressed wheat plants. They also reported that GB can alter the adaptive responses of wheat to drought; they virtually negate the cell-membrane (plasmalemma) stability associated with drought stress conditioned wheat, and diminish solute potentials to below those for the drought stress only treatments; water potential, however, was not altered by GB infestations. As would be expected, osmotic adjustment (the maintenance of turgor through the accumulation of solutes in plants under drought stress) was also reduced by GB. These data provide physical and physiological evidence supporting field observations that GB infestations are potentially more damaging when wheat is subjected to drought. A recent study by Riedell (1989) indicates that RWA infestation limits the ability of barley plants to adjust osmotically to drought stress. In particular, plants previously infested with RWA possessed a decreased ability to maintain leaf relative water content in response to drought stress.

Limited research has been conducted to elucidate the interacting effects of host plant characteristics (as influenced by plant cultivar) on aphid parasitoid efficiency in limiting aphid population growth and preventing aphid induced plant biotic stress. Although some progress has been made in understanding the effects of water deficits on small grain cereals and their aphids, there remains a great void in determining how aphids and drought stress interact. Furthermore, I am unaware of any studies that have focused on the effects of drought stress on a third trophic level comprised of aphid parasitoids. My overall goal in this research was to unravel the interacting influences of plant water deficits, host plant resistance, and cereal aphids on parasitoid population dynamics and biological control efficacy.

REFERENCES

Andjei, G.B. and M.B. Kirkham. 1980. Evaluation of winter wheat cultivars for drought resistance. Euphytica. 29: 155-60.

Archer, T.L., R.H. Cate, R.D. Eikenbary and K.J. Starks. 1974. Parasitoids collected from greenbugs and corn leaf aphids in Oklahoma in 1972. Ann. Entomol. Soc. Amer. 67: 11-14.

Argandoña, V.H., H.M. Niemeyer and L.J. Corcuera. 1981. Effect of content and distribution of hydroxamic acids in wheat on infestation by the aphid Schizaphis graminum. Phytochem. 20: 673-676.

Auclair, J.L. 1989. Host plant resistance. Pages 225-265 in: Aphids: Their Biology, Natural Enemies and Control, A.K. Minks and P. Harrewijn, Eds. World Crop Pests 2C, Elsevier, Amsterdam.

Begg, J.E. and N.C. Turner. 1976. Crop water deficits. Advan. in Agron. 28: 161-217.

Bergman, J.M. and W.M. Tingey. 1979. Aspects of interaction between plant genotypes and biological control. Bull. Entomol. Soc. Amer. 25: 275-279.

Bergman, D.K., J.W. Dillwith, R.K. Campbell and R.D. Eikenbary. 1990. Cuticular hydrocarbons of the Russian wheat aphid. Southwestern Entomol. 15: 91-100.

Boethel, D.J. and R.D. Eikenbary, Eds. 1986. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Wiley, New York. 224 pp.

Bush, L., J.E. Slosser, W.D. Worrall and G.J. Puterka. 1987. Status of greenbug biotypes in Texas. Southwestern Entomol. 12: 229-235.

Burton, R.L. 1986. Effect of greenbug (Homoptera: Aphididae) damage on root and shoot biomass of wheat seedlings. J. Econ. Entomol. 79: 633-636.

Butts, P.A. and K.W. Pakendorf. 1984. Wheat breeding for resistance to Diuraphis noxia: methodology and progress. Pages 47-52 in: M.C. Walters, Ed. Progress in Russian Wheat Aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa. Tech. Commun. Dep. Agric. Repub. S. Afr. 191.

Campbell, R.K., R.D. Eikenbary, M.F. Schuster, M.C. Lidell, K.E. Godfrey and G.L. Teetes. 1990a. Pests of small grains and grain sorghum. Pages 67-77 in: D.H. Habeck, F.D. Bennett and J.H. Frank. Eds. Classical Biological Control in the Southern United States. South. Coop. Ser. Bull. 355.

Campbell, R.K., C.E. Salto, L.C. Sumner and R.D. Eikenbary. 1990b. Tritrophic interactions between grains, the greenbug (Schizaphis graminum) and entomophaga. Pages 393-401 in: A. Szentesi and T. Jermy, Eds. Insects - Plants '89. (Symp. Biol. Hungary 39). Akadémiai Kiadó, Budapest.

Carver, M. 1989. Biological control of aphids. Pages 141-166 in: Aphids: Their Biology, Natural Enemies and Control, A.K. Minks and P. Harrewijn, Eds. World Crop Pests 2C, Elsevier, Amsterdam.

Corcuera, L.J. 1984. Effects of indole alkaloids from Gramineae on aphids. Phytochem. 23: 539-541.

Day, W., D.W. Lawlor and B.J. Leggs. 1981. The effects of drought on barley: soil and plant water relations. J. Agri. Sci. 96: 61-78.

Dorschner, K. W., R. C. Johnson, R. D. Eikenbary and J. D. Ryan. 1986. Insect-plant interactions: greenbugs (Homoptera: Aphididae) disrupt acclimation of winter wheat to drought stress. Environ. Entomol. 15: 118-121.

Dreyer, D.L. and K.C. Jones. 1981. Feeding deterrency of flavonoids and related phenolics towards Schizaphis graminum and Myzus persicae: Aphid feeding deterrents in wheat. Phytochem. 20: 2489.

Duffey, S.S., K.A. Bloem and B.C. Campbell. 1986. Consequences of sequestration of plant natural products in plant-insect-parasitoid interactions. Pages 31-60 in: D. J. Boethel and R. D. Eikenbary, Eds. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Ellis Horwood Ltd.

Du Toit, F. 1987. Resistance in wheat (Triticum aestivum) to Diuraphis noxia (Hemiptera: Aphididae). Cereal Res. Commun. 15: 175-179.

Du Toit, F. 1988. Another source of Russian wheat aphid (Diuraphis noxia) resistance in Triticum aestivum. Cereal Res. Commun. 16: 105-106.

Du Toit, F. and M.C. Walters. 1984. Damage assessment and economic threshold values for the chemical control of the Russian wheat aphid, Diuraphis noxia (Mordvilko) on winter wheat. Pages 58-62 in: M.C. Walters, Ed. Progress in Russian Wheat Aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa. Tech. Commun. Dep. Agric. Repub. S. Afr. 191.

van Emden, H.F. 1988. The potential for managing indigenous natural enemies of aphids on field crops. Phil. Trans. R. Soc. Lond. B. 318: 183-201.

van Emden, H.F. and C.H. Wearing. 1965. The role of the aphid host plant in delaying economic damage levels in crops. Ann. Appl. Biol. 56: 323-324.

Frank, W.A., R.A. Scott, J.E. Slosser and W.D. Worrall. 1989. Resistance in triticale to Russian wheat aphid and greenbug. Southwestern Entomol. 14: 167-178.

Gilchrist, L.I., R. Rodriguez and P.A. Burnett. 1984. The extent of freestate streak and Diuraphis noxia in Mexico. Pages 157-163 in: Barley yellow dwarf, a proceedings of the workshop. International Maize and Wheat Improvement Center (CIMMYT), Mexico City.

Gilstrap, F.E. 1990. Biological control of RWA - importation of agents in 1989. Page 4 in: L.D. Charlet, Ed. International Organization for Biological Control, Nearctic Regional Section Newsletter, No. 34, Summer 1990.

Gilstrap, F.E., and L.K. McKinnon. 1988. Response of native parasites to Russian wheat aphid. Texas Agric. Exp. Sta. PR-4558. 5pp.

Hamilton, G.C., R.L. Kirkland, and I.D.R. Peries. 1982. Population ecology of Schizaphis graminum (Rondani) (Homoptera: Aphididae) on grain sorghum in Central Missouri. Environ. Entomol. 11: 618-628.

Harvey, T.L. and H.L. Hackerott. 1969. Recognition of a greenbug biotype injurious to sorghum. J. Econ. Entomol. 62: 776-779.

Harvey, T.L. and T.J. Martin. 1990. Resistance of Russian wheat aphid, Diuraphis noxia, in wheat, (Triticum aestivum). Cereal Res. Comm. 18: 127-129.

Hein, G., L. Brooks, G. Johnson, B. Massey, D. McBride, P. Morrison, J.F. Schultz, E. Spackman and F. Peairs. 1990. Economic impact of the Russian wheat aphid in the western United States: 1988-1989. Great Plains Agric. Council Pub. 10pp.

Hewitt, P.H, G.J.J. Van Niekerk, M.C. Walters, C.F. Kriel and A. Fouche. 1984. Aspects of the ecology of the Russian wheat aphid, Diuraphis noxia, in the Bloemfontein district. I. The colonization and infestation of sown wheat, identification of summer hosts and cause of infestation symptoms. Pages 3-13 in: M.C. Walters, Ed. Progress in Russian Wheat Aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa. Tech. Commun. Dep. Agric. Repub. S. Afr. 191.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24: 519-570.

Jackson, H.B., L.W. Coles, E.A. Wood, Jr. and R.D. Eikenbary. 1970. Parasites reared from the greenbug and corn leaf aphid in Oklahoma in 1968 and 1969. J. Econ. Entomol. 63: 733-736.

Keim, D.L. and W.E. Kronstad. 1980. Drought response of winter wheat cultivars grown under field stress conditions. Crop. Sci. 21: 11-15.

Kennedy,J.S., A. Ibbotson and C.O. Booth. 1950. The distribution of aphid infestation in relation to leaf age. I. Myzus persicae and Aphis fabae on spindle trees and sugar beet plants. Ann. Appl. Biol. 37: 651-679.

Kennedy, J.S., K.P. Lamb and C.O. Booth. 1958. Responses of Aphis fabae to water shortage in host plants in pots. Ent. Exp. Appl. 1: 274-291.

Kerns, D.L., D.C. Peters and G.J. Puterka. 1987. Greenbug biotype and grain sorghum seed sale surveys in Oklahoma, 1986. Southwestern Entomol. 12: 237-243.

Kindler, S.D. and S.M. Spomer. 1986. Biotypic status of six greenbug (Homoptera: Aphididae) isolates. Environ. Entomol. 15: 567-572.

Kindler, S.D. and R. Staples. 1970. The influence of fluctuating and constant temperatures, photoperiod and soil moisture on the resistance of alfalfa to spotted alfalfa aphid. J. Econ. Entomol. 63: 1198-1201.

Kuo, H.L. 1986. Resistance of oats to cereal aphids: Effects on parasitism by Aphelinus asychis (Walker). Pages 125-137 in: D.J. Boethel and R.D. Eikenbary, Eds., Interactions of Plant Resistance and Parasitoids and Predators of Insects. Ellis Horwood Ltd., Chichester.

Levitt, J. 1980. Responses of plants to environmental stresses. Vol. II. Academic Press, Inc. New York. 697 pp.

McMurtry, J.A. 1962. Resistance of alfalfa to spotted alfalfa aphid in relation to environmental factors. Hilgardia. 32: 501-539.

Michels, G.J., Jr. 1986. Graminaceous North American host plants of the greenbug with notes on biotypes. Southwest. Entomol. 11: 55-66.

Michels, G.J., Jr. and D.J. Undersander. 1986. Temporal and spatial distribution of the greenbug (Homoptera: Aphididae) on sorghum in relation to water stress. J. Econ. Entomol. 79: 1221-1225.

Michels, G.J., Jr., T.J. Kring, R.W. Behle, A.C. Bateman and N.M. Heiss. 1987. Development of greenbug (Homoptera: Aphididae) on corn: geographic variations in host-plant range of biotype E. J. Econ. Entomol. 80: 394-397.

Mittler, T.E. 1958. Studies on the feeding and nutrition of Tuberolachnus salignus. II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. J. Exp. Biol. 35: 626-638.

Morrison, P. 1988. The Russian wheat aphid. Pages 37-39 in: S. Coppock and B. Massey, Eds. Proc. of the First Russian Wheat Aphid Conf. Coop. Ext. Serv. Bull. E-875, Okla. State Univ.

Pettersson,. J. 1971. Studies on four grass-inhabiting species of Schizaphis (Homoptera: Aphididae). III. Host plants. Swedish J. Agric. Res. 1: 133-138.

de Ponti, O.M.B. 1980. Breeding glabrous cucumber (Cucumis sativus) varieties to improve the biological control of the greenhouse whitefly (Trialeurodes vaporariorum). Pages 197-199 in: A.K. Minks and P. Gruys, Eds. Integrated Control of Insect Pests in the Netherlands. Pudoc, Wageningen.

Puterka, G.J. and D.C. Peters. 1988. Rapid technique for determining greenbug (Homoptera: Aphididae) biotypes B, C, E, and F. J. Econ. Entomol. 81: 396-399.

Puterka, G.J., D.C. Peters, D.L. Kerns, J.E. Slosser, L. Bush, D.W. Worrall, and R.W. McNew. 1988. Designation of two new greenbug (Homoptera: Aphididae) biotypes G and H. J. Econ. Entomol. 81: 1754-1759.

Puterka, G.J., J.D. Burd, and R.L. Burton. 1992. Biotypic variation in a worldwide collection of the Russian wheat aphid. J. Econ. Entomol. 85: (in press).

Quarrie, S.A. 1980. Genotypic differences in leaf water potential, abscisic acid, and proline concentration in spring wheat during drought stress. Ann. Bot. (Lond.) 46: 383-394.

Quick, J.S. 1989. Developing RWA resistant wheat varieties. Page 14 in: Proc. Russian Wheat Aphid Conf., Albuquerque, New Mexico, Oct. 25-27, 1989. New Mexico State Univ.

Reed, D.K., J.A. Webster, B.G. Jones and J.D. Burd. 1991. Tritrophic relationships of Russian wheat aphid (Homoptera: Aphididae), a hymenopterous parasitoid (Diaeretiella rapae McIntosh), and resistant and susceptible small grains. Biological Control 1: 35-41.

Riedell, W.E. 1989. Effects of Russian wheat aphid infestation on barley plant response to drought stress. Physiol. Plant. 77: 587-592.

Salto, C.E., R.D. Eikenbary and K.J. Starks. 1983. Compatibility of Lysiphlebus testaceipes (Hymenoptera: Braconidae) with greenbug (Homoptera: Aphididae) biotypes C and E reared on susceptible and resistant oat varieties. Environ. Entomol. 12: 603-604.

Schuster, D.J. and K.J. Starks. 1975. Preference of Lysiphlebus testaceipes for greenbug resistant and susceptible small grain species. Environ. Entomol. 4: 887-888.

Starks, K.J., R. Muniappan and R.D. Eikenbary. 1972. Interaction between plant resistance and parasitism against the greenbug on barley and sorghum. Ann. Entomol. Soc. Am. 65: 650-655.

Stoetzel, M.B. 1987. Information on and identification of Diuraphis noxia (Homoptera: Aphididae) and other aphid species colonizing leaves of wheat and barley in the United States. J. Econ. Entomol. 80: 696-704.

Sumner, L.C., J.T. Need, R.W. McNew, K.W. Dorschner, R.D. Eikenbary and R.C. Johnson. 1983. Response of Schizaphis graminum (Homoptera: Aphididae) to drought-stressed wheat, using polyethylene glycol as a matricum. Environ. Entomol. 12: 919-922.

Sumner, L.C., K.W. Dorschner, J.D. Ryan, R.D. Eikenbary, R.C. Johnson and R.W. McNew. 1986a. Reproduction of *Schizaphis graminum* (Homoptera: Aphididae) on resistant and susceptible wheat genotypes during simulated drought stress induced with polyethylene glycol. Environ. Entomol. 15: 756-762.

Sumner, L.C., R.D. Eikenbary and R.C. Johnson. 1986b. Survival and reproduction of *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae) on winter wheat during simulated drought stress. J. Kan. Entomol. Soc. 59: 561-563.

Taylor, C.E. 1955. Growth of the potato plant and aphid colonization. Ann. Appl. Biol. 43: 151-155.

USDA. 1977. Preventing greenbug outbreaks. USDA-SEA Leaflet No. 309. 11pp.

Walters, M.C., Ed. Progress in Russian Wheat Aphid (*Diuraphis noxia* Mordw.) Research in the Republic of South Africa. Tech. Commun. Dep. Agric. Repub. S. Afr. 191. 78pp.

Wearing, C.H. and H.F. van Emden. 1967. Studies on the relations of insect and host plants on infestations by *Aphis fabae* (Scop.), *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.) Nature (London). 213: 1051-1052.

Webster, J.A. 1989. Detection of RWA resistance in rye and barley. Pages 18-19 in: Proc. Russian Wheat Aphid Conference, Albuquerque, New Mexico, Oct. 25-27, 1989. New Mexico State Univ.

Webster, J.A. 1990. Resistance in triticale to the Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 83: 1091-1095.

Webster, J.A., K.J. Starks and R.L. Burton. 1987. Plant resistance studies with *Diuraphis noxia* (Homoptera: Aphididae), a new United States wheat pest. J. Econ. Entomol. 80: 944-949.

Webster, J.A., C.A. Baker and D.R. Porter. 1991. Detection and mechanisms of Russian wheat aphid (Homoptera: Aphididae) resistance in barley. J. Econ. Entomol. 84: 669-673.

Zohdy, N.Z.M. 1976. On the effect of the food of *Myzus persicae* (Sulz.) on the hymenopterous parasite *Aphelinus asychis* Walker. Oecologia. 26: 185-191.

PART II

TRITROPHIC INTERACTIONS BETWEEN WHEAT, APHIDS AND A PARASITOID

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), has long been considered one of the most injurious insect pests attacking grains in the United States. This aphid possesses a wide host range (Pettersson 1971, Michels 1986), but in recent years it has been expanding its adaptive range to colonize both new host species such as grain sorghum (Harvey and Hackerott 1969) as well as formerly resistant crop cultivars released from germplasm enhancement programs. A number of greenbug biotypes have been defined based on their ability to differentially damage greenbug resistance sources in wheat, sorghum, oats, rye, and barley (see Puterka et al. 1988). The most agronomically important and prevalent greenbug biotypes in the field are C (GBC) and E (GBE) (Bush et al. 1987, Kerns et al. 1987).

The parasitoid Lysiphlebus testaceipes (Cresson) is the most abundant and recurrent natural enemy of the greenbug in the U.S. (Jackson et al. 1970, Archer et al. 1974). It has also been shown to complement host plant resistance (HPR) in the field (Hamilton et al. 1982).

The Russian wheat aphid (RWA), Diuraphis noxia (Mordvilko) is a new and serious pest of small grains in the U.S. which was first found in Texas in 1986 (Stoetzel 1987). L. testaceipes can parasitize RWA in the field (Morrison

1988), yet laboratory studies indicate that it greatly prefers the greenbug (Gilstrap and McKinnon 1988). Commonly used wheat (*Triticum aestivum* L.) varieties, including those resistant to certain greenbug biotypes, do not possess significant levels of resistance to the RWA (Webster et al. 1987) though some resistance sources are available in lines of triticale (x*Triticosecale*) (Frank et al. 1989, Webster 1990).

HPR and biological control (BC) are often considered compatible pest management strategies (Bergman and Tingey 1979, see Boethel and Eikenbary 1986). When both control methodologies are used concurrently, unrelated mortality effects are applied, which reduces the potential rate of genetic adaptation in the pest population to selection pressures imposed by resistant germplasms, thus possibly slowing the development of new pest biotypes. However, parasitoid performance may be detrimentally altered by the host plant of the pest insect if resistance is based upon significant chemical antibiosis. Although different species of host plants can produce the greatest range in responses, cultivars of the same species can also differentially affect parasitoid success (de Ponti 1980). Furthermore, four trophic level interactions, which include hyperparasitoids, must also be considered (Orr and Boethel 1986). Starks et al. (1972) found resistant varieties of barley, (*Hordeum vulgare* L.) and sorghum, (*Sorghum bicolor* Moench), to be complementary with the effect of *L. testaceipes* on greenbugs in laboratory studies, although the complementary effect was not evident in caged field studies using sorghum (Starks et al. 1974). Schuster and Starks (1975) showed a resistant oat (Avena sativa L.) line was more attractive to L. testaceipes than a susceptible variety in olfactometer tests but no such differences occurred with resistant and susceptible sorghum. Salto et al. (1983) found no differences in the parasitization rate of greenbug on resistant and susceptible oats. Kuo (1986) concluded that oat resistance to cereal aphids and the effect of an aphid parasitoid seem to complement each other in reducing the number of aphids. I am unaware of any similar studies conducted on resistant and susceptible wheat varieties. The objective of this research was to further investigate such tritrophic interactions using wheat; the aphids GBC, GBE and RWA; and L. testaceipes.

MATERIALS AND METHODS

This experiment was designed to compare the interacting effects of GBC, GBE, or RWA and L. testaceipes when reared on resistant and susceptible wheat varieties. 'TAM 107' is resistant to GBC but exhibits little or no resistance to GBE and RWA , whereas 'TAM 105' is susceptible to GBC, GBE and RWA (Porter 1982, Webster et al. 1987). Experiments were performed in growth chambers at a constant 22° C and a 14 hour photophase. Plants were cultured in a standard soil mixture in 7.5 cm diameter plastic pots and were regularly watered to maintain a high water status. The experimental units consisted of one caged plant (1-2 leaf stage, GS 11-12, Zadoks et al. 1974) infested with one first instar aphid. The time of aphid infestation was considered Day 0. Those plant treatments that included the parasitoid effect received one mating pair of L. testaceipes on Day 8. The experimental protocol was a lattice design with five replications and was analyzed as a factorial. Aphid population growth was monitored alternating days for 30 d or until plant death; plant death generally coincided with a downturn in aphid population numbers. At this time, root and shoot dry weights were obtained.

RESULTS AND DISCUSSION

Figure 1 illustrates GBC population growth curves on resistant ('TAM 107') and susceptible ('TAM 105') wheat varieties with and without the presence of L. testaceipes. The resistant wheat alone extended mean plant survival from 18 to 28 days, however the protracted survival period facilitated a substantially higher aphid population. Comparing the susceptible responses, parasitoid presence extended plant survival four days but did not significantly influence the peak aphid population. The combination of resistant wheat and parasitoid presence substantially reduced aphid numbers and would have driven the aphids to extinction within the closed system had the experiment not been terminated on Day 30. This was evident by the large number of parasitoid mummies and relatively few reproducing aphids present on these plants by Day 30.

The basic lack of resistance of 'TAM 107' to GBE is evident if the left graph of Figure 2 is compared to the left graph of Fig. 1. The combination of parasitoid presence and 'TAM 107 substantially extended plant survival but the lack of GBE resistance is evidenced by a rapid increase in aphid numbers. The increase in aphid population resulted in plant damage to a level at which the parasitoid alone was incapable of preventing.

Russian wheat aphid population growth curves are presented in Fig. 3. Neither the GBC resistant 'TAM-107' nor the presence of L. testaceipes had a suppressive effect on RWA populations. The 'TAM 107' did not affect RWA population growth and L. testaceipes rarely oviposited in RWA, which corroborates the results of Gilstrap and McKinnon (1988). In contrast to greenbugs, the large populations of RWA caused substantially less plant damage based on plant survival times.

Oven dried plant biomass values for the different treatment combinations are shown in Table 1. The 'TAM 107' wheat cultivar generally attained a greater size than 'TAM 105' over the course of this experiment. The RWA, in particular, seriously limits root biomass production. With the greenbug, parasitoid presence or plant resistance may help to preserve biomass productivity. Here again, however, no helpful parasitoid effect can be seen with RWA.

Unfortunately, a widely used greenbug (GBC) resistant wheat and the most ubiquitous cereal aphid parasitoid in the U.S. were ineffective against the RWA in these experiments. The need for more effective RWA resistance sources for introduction into commercial cereal varieties and a more efficacious RWA parasitoid in the U.S. is clearly evident.

REFERENCES

Archer, T.L., R.H. Cate, R.D. Eikenbary and K.J. Starks. 1974. Parasitoids collected from greenbugs and corn leaf aphids in Oklahoma in 1972. Ann. Entomol. Soc. Amer. 67: 11-14.

Boethel, D.J. and R.D. Eikenbary. 1986. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Ellis Horwood Ltd., Chichester, U.K. 224pp.

Bergman, J.M. and W.M. Tingey. 1979. Aspects of interaction between plant genotypes and biological control. Bull. Entomol. Soc. Amer. 25: 275-279.

Bush, L., J.E. Slosser, W.D. Worrall and G.J. Puterka. 1987. Status of greenbug biotypes in Texas. Southwestern Entomol. 12: 229-235.

Frank, W.A., R.A. Scott, J.E. Slosser and W.D. Worrall. 1989. Resistance in triticale to Russian wheat aphid and greenbug. Southwestern Entomol. 14: 167-178.

Gilstrap, F.E. and L.K. McKinnon. 1988. Response of native parasites to Russian wheat aphid. Texas Agric. Exp. Sta. PR-4558. 5pp.

Hamilton, G.C., R.L. Kirkland and I.D.R. Peries. 1982. Population ecology of Schizaphis graminum (Rondani) (Homoptera: Aphididae) on grain sorghum in central Missouri. Environ. Entomol. 11: 618-628.

Harvey, J.L. and H.L. Hackerott. 1969. Recognition of a greenbug biotype injurious to sorghum. J. Econ. Entomol. 62: 776-779.

Jackson, H.B., L.W. Coles, E.A. Wood, Jr. and R.D. Eikenbary. 1970. Parasites reared from the greenbug and corn leaf aphid in Oklahoma in 1968 and 1969. J. Econ. Entomol. 63: 733-736.

Kerns, D.L., D.C. Peters and G.J. Puterka. 1987. Greenbug biotype and grain sorghum seed sale surveys in Oklahoma, 1986. Southwestern Entomol. 12: 237-243.

Kuo, H.L. 1986. Resistance of oats to cereal aphids: Effects on parasitism by Aphelinus asychis (Walker).

Pages 125-137 in: D.J. Boethel and R.D. Eikenbary, Eds. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Ellis Horwood Ltd., Chichester, U.K.

Michels, G.J., Jr. 1986. Graminaceous North American host plants of the greenbug with notes on biotypes. Southwestern Entomol. 11: 55-66.

Morrison, P. 1988. The Russian wheat aphid. Pages 37-39 in: S. Coppock and B. Massey, Eds. Proc. of the First Russian Wheat Aphid Conference. Coop. Ext. Serv. Bull. E-875, Okla. State Univ., Stillwater, OK.

Orr, D.B. and D.J. Boethel. 1986. Influence of plant antibiosis through four trophic levels. Oecologia (Berlin) 70: 242-249.

Petterson, J. 1971. Studies on four grass-inhabiting species of Schizaphis (Homoptera: Aphididae). III. Host plants. Swedish J. Agric. Res. 1: 133-138.

de Ponti, O.M.B. 1980. Breeding glabrous cucumber (Cucumis sativus) varieties to improve the biological control of the greenhouse whitefly (Trialeurodes vaporariorum). Pages 197-199 in: A.K. Minks and P. Gruys, Eds. Integrated Control of Insect Pests in The Netherlands. Pudoc, Wageningen.

Porter, K.G., G.L. Peterson and O. Vise. 1982. A new greenbug biotype. Crop Sci. 22: 847-850.

Puterka, G.J., D.C. Peters, D.L. Kerns, J.E. Slosser, L. Bush, D.W. Worrall and R.W. McNew. 1988. Designation of two new greenbug (Homoptera: Aphididae) biotypes G and H. J. Econ. Entomol. 81: 1754-1759.

Salto, C.E., R.D. Eikenbary and K.J. Starks. 1983. Compatibility of Lysiphlebus testaceipes (Hymenoptera: Braconidae) with greenbug (Homoptera: Aphididae) biotypes C and E reared on susceptible and resistant oat varieties. Environ. Entomol. 12: 603-604.

Schuster, D.J. and K.J. Starks. 1975. Preference of Lysiphlebus testaceipes for greenbug resistant and susceptible small grain species. Environ. Entomol. 4: 887-888.

Starks, K.J., R. Muniappan and R.D. Eikenbary. 1972. Interaction between plant resistance and parasitism against the greenbug on barley and sorghum. Ann. Entomol. Soc. Amer. 65: 650-655.

Starks, K.J., E.A. Wood, Jr. and R.L. Burton. 1974. Relationships of plant resistance and Lysiphlebus testaceipes to population levels of the greenbug on grain sorghum. Environ. Entomol. 3: 950-952.

Stoetzel, M.B. 1987. Information on and identification of Diuraphis noxia (Homoptera: Aphididae) and other aphid species colonizing leaves of wheat and barley in the United States. J. Econ. Entomol. 80: 696-704.

Webster, J.A. 1990. Resistance in triticale to the Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 83: 1091-1095.

Webster, J.A., K.J. Starks and R.L. Burton. 1987. Plant resistance studies with Diuraphis noxia (Homoptera: Aphididae), a new United States wheat pest. J. Econ. Entomol. 80: 944-949.

Zadoks, J.C., T.T. Chang and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14: 415-421.

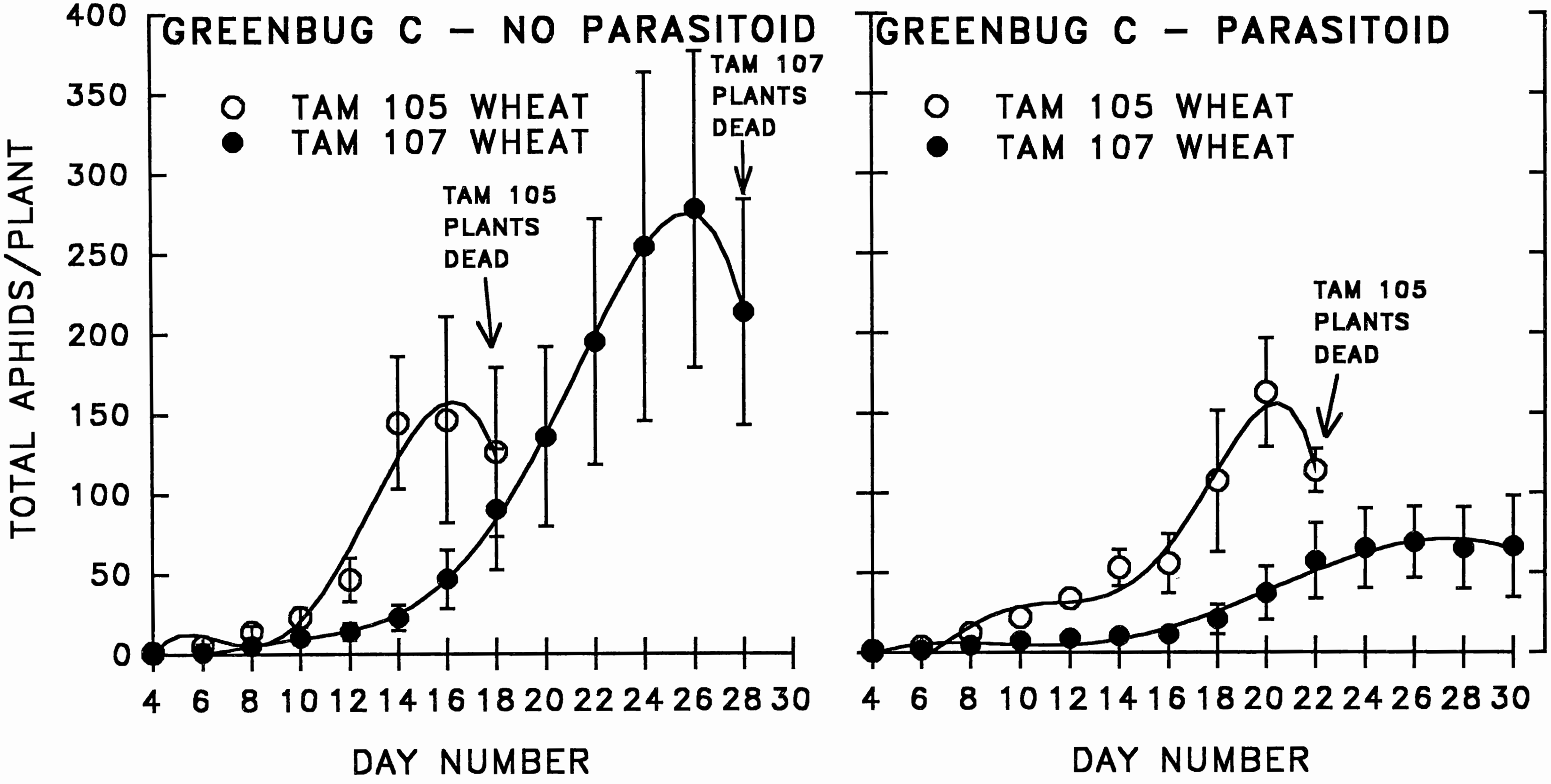

Figure 1. Populations of greenbug biotype C with and without L. testaceipes introduced Day 8. TAM 105 wheat susceptible, TAM 107 wheat resistant. Means ± SEM.

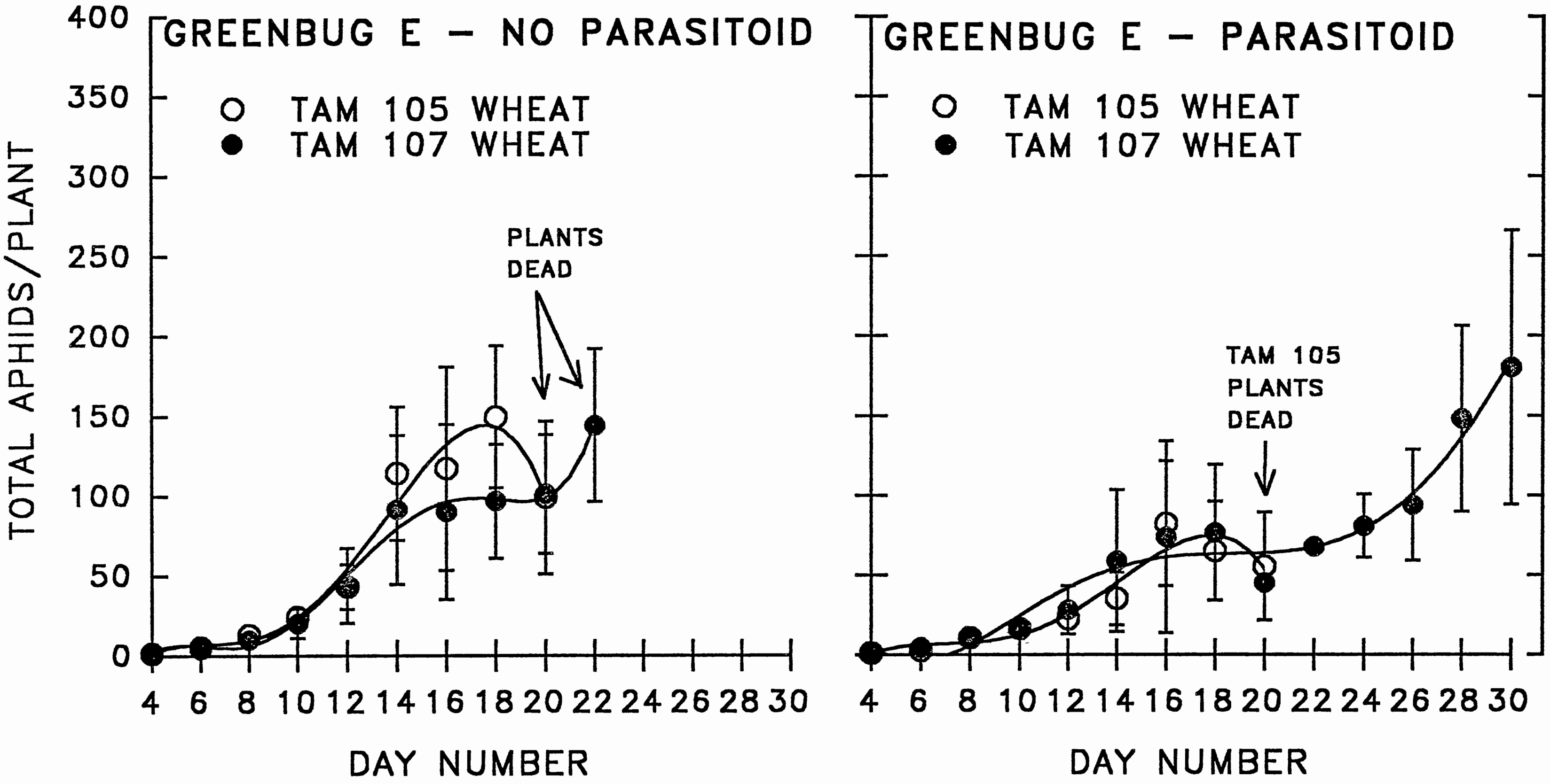

Figure 2. Populations of greenbug biotype E with and without *L. testaceipes* introduced Day 8. Both TAM 105 and TAM 107 wheats susceptible. Means ± SEM.

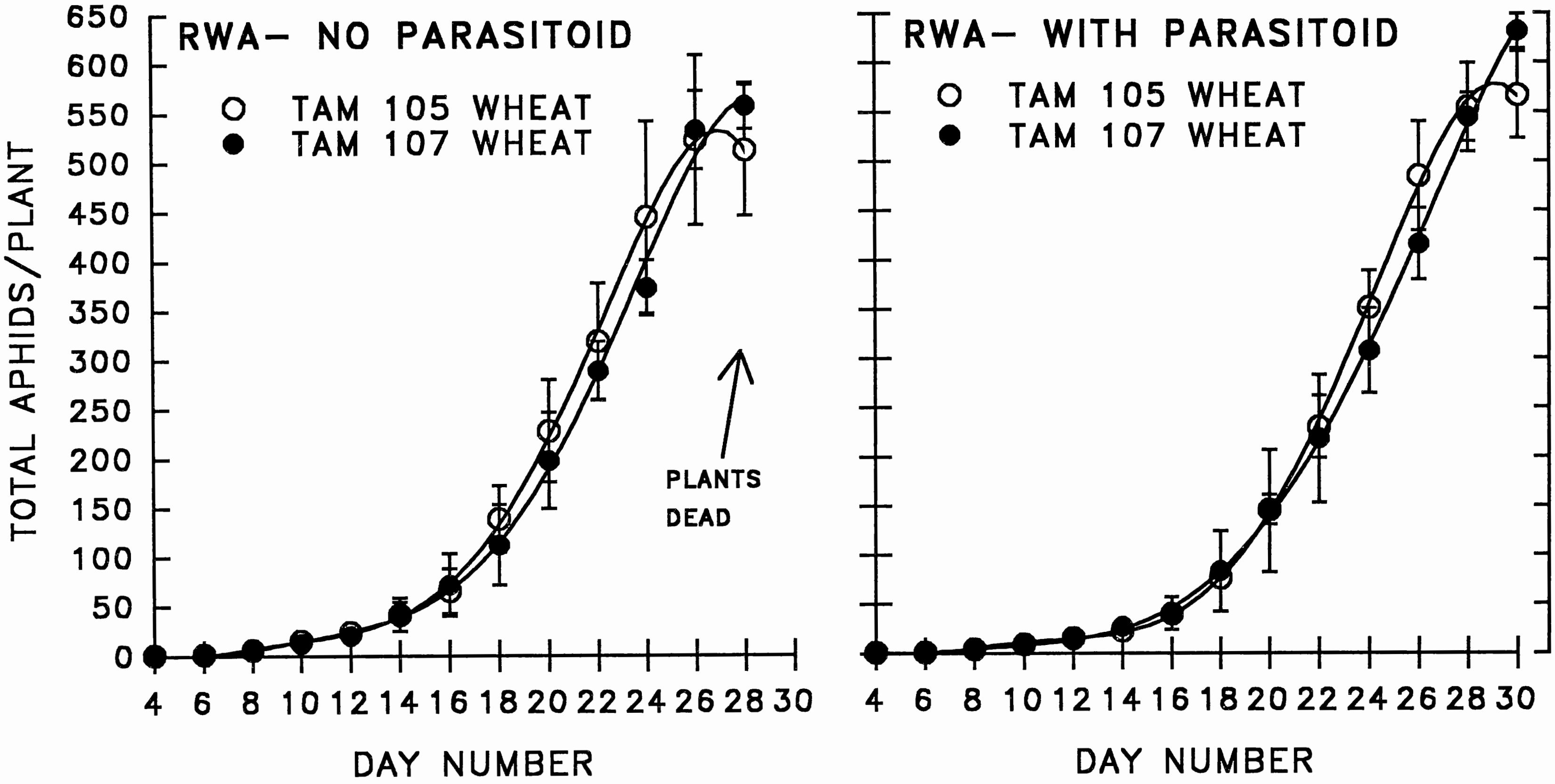

Figure 3. Populations of Russian wheat aphid with and without _L. testaceipes_ introduced Day 8. Both TAM 105 and TAM 107 wheats susceptible. Means ± SEM.

TABLE 1

Summary of Mean Values (SEM) for Dried Plant Biomass on Day of Plant Death or Termination of Experiment

	Wheat Cultivar			
Treatment	**TAM-105**		**TAM-107**	
	Root Wt (mg)	**Shoot Wt (mg)**	**Root Wt (mg)**	**Shoot Wt (mg)**
Control	38 (10)	92 (16)	52 (11)	107 (15)
Greenbug C	14 (2)	36 (7)	36 (11)	72 (16)
Greenbug C - P	12 (2)	36 (8)	40 (7)	110 (12)
Greenbug E	12 (2)	36 (8)	28 (7)	54 (14)
Greenbug E - P	20 (6)	54 (18)	40 (11)	106 (21)
Russian Wheat Aphid	14 (4)	46 (7)	16 (2)	62 (11)
Russian Wheat Aphid - P	10 (2)	46 (6)	18 (5)	58 (4)

Control = no aphids; aphid designations followed by "P" indicate parasitoid introduced Day 8.

PART III

RUSSIAN WHEAT APHID AND DROUGHT STRESSES IN WHEAT: TRITROPHIC INTERACTIONS WITH PLANT RESISTANCE AND A PARASITOID

INTRODUCTION

The Russian Wheat Aphid (RWA), Diuraphis noxia (Mordvilko), has become a serious pest of grains in North America (Hein et al. 1990). Heavily infested plants exhibit striking damage symptoms including prostrate growth, interveinal bleaching, and diminished leaf expansion caused by impaired cell wall extensibility (Burd et al. 1989, 1992). Such unexpanded (rolled) leaves serve as refugia for the aphid colonies thus limiting effective search and attack by aphid parasitoids.

Interest in the interactions of host plant resistance and biological control, ie. tritrophic interactions, has been expanding rapidly in recent years. This has been true for both insect pests in general (Boethel and Eikenbary 1986) and for aphids in particular (van Emden and Wratten 1991, van Lenteren 1991). Initial investigations on tritrophic interactions with RWA were included in a study focused primarily on the greenbug, Schizaphis graminum (Rondani) (Campbell et al. 1990). However, because the parasitoid used was a greenbug adapted strain of Lysiphlebus testaceipes (Cresson) it proved incapable of effectively parasitizing the RWA and the greenbug resistant wheat (Triticum aestivum L.) used exhibited no significant resistance to RWA. More recently, Reed et al. (1991) found that an antibiotic RWA resistant triticale (x*Triticosecale*) (PI 386148) detrimentally affected the growth and reproduction of both the RWA and one of its parasitoids, *Diaeretiella rapae* McIntosh. They also showed that a tolerant RWA resistant wheat (PI 372129) was beneficial for parasitoid action because the extent of leaf rolling was substantially reduced.

Drought and aphid infestations of cereal crops often occur together or sequentially during the growing season, yet few studies have investigated interactions of grain aphids and drought stressed grains. Sumner et al. (1983) found that wheat stressed with polyethylene glycol (PEG) reduced the fecundity and longevity of greenbug biotype C (GBC) when the plants were osmotically stressed to below a critical threshold. A subsequent study (Sumner et al. 1986a) analyzed the response of GBC to controlled levels of PEG induced osmotic stress on GBC resistant (OK 80268) and susceptible (cv. Sturdy) wheat. They reported that greenbug longevity (days to death) was not altered by the host plant but was significantly decreased by the PEG induced water stress. However, GBC fecundity was highly dependent upon the host plant, and was significantly reduced on the GBC resistant cultivar. Moreover, water stress reduced GBC fecundity on the susceptible wheat to levels equal to or lower than those for the non-stressed resistant entry. The simulated stress also significantly reduced GBC fecundity on the resistant wheat. Similar studies on wheat using the corn leaf aphid, Rhopalosiphum maidis (Fitch), showed that fecundity, longevity and the reproductive period of the aphid declined linearly with increasing osmotic stress levels (Sumner et al. 1986b). Michels and Undersander (1986) found that greenbug reproduction was reduced on water stressed field grown grain sorghum, (Sorghum bicolor (L.) Moench. Similar results were obtained by Dorschner et al. (1986) in growth chamber experiments where greenbug densities (number of greenbug per mg shoot dry weight) were greater on drought-stressed wheat plants. Riedell (1989) found that RWA infestation of barley, (Hordeum vulgare L.), plants limits the plants' ability to adjust osmotically to subsequent drought stress. In particular, plants previously infested with RWA have a decreased ability to adjust osmotically and thereby maintain adequate leaf relative water content in response to drought stress.

Although some progress has been made in understanding the effects of water deficits on grains and their aphids, there still remains a great void in determining how cereal aphids and drought stresses interact with different grain species. Virtually nothing is known of the interactions of drought, RWA, plant resistance and biological control. This study was undertaken to investigate these interactions using seedlings of a susceptible wheat cultivar ('TAM W-101') (Webster 1990), a wheat line which was the first to exhibit significant RWA resistance in U. S. screening trials (PI

372129) (Quick 1989), RWA and a Syrian strain of the parasitoid D. rapae.

MATERIALS AND METHODS

The experiment was conducted in a greenhouse during June and July with supplemental metal halide lighting to provide a 14 h photophase. Temperatures were controlled at 25 ± 5° C. Individual plants were grown from pre-germinated seed in a fritted clay medium (Absorb-N-Dry, Balcones Minerals, Flatonia, Tex.) in cone-tainers (Supercell Cone-Tainer, Ray Leach Cone-Tainer Nursery, Canby, Ore.) (Burton 1986). Plants were infested with 25 mature apterous RWA at the 3-leaf stage (GS 13, Zadoks et al. 1974) and both infested and control plants were caged with ventilated clear plastic cages. Main effect treatments included combinations of plant resistance, drought, RWA infestation, and D. rapae and were replicated 15 times. Plants subjected to drought stress treatments received only minimal amounts of maintenance water while non-stressed plants were regularly watered to capacity. All plants were fertilized biweekly with Peters' Complete Peat-Lite Special (analysis 15-16-17) (Peters Fertilizer Products, Fogelsville, Penn.). Those treatments receiving parasitoids received one mating pair of D. rapae 9 d after aphid infestation. The parasitoids were removed after 24 h. The experiment was continued for an additional 10 d to provide a sufficient time for the formation of the F1 parasitoid mummies. Subsequently, the experiment was terminated and a number of plant, aphid and parasitoid parameters measured.

Leaf water status of ten replicates from each treatment combination was measured by excising 0.24 cm^2 leaf discs from 3 cm above the base of the second fully expanded leaf on the main stem of each plant using leaf-cutter psychrometers (J.R.D. Merrill Specialty Equipment, Logan, Utah). Water potential, osmotic potential, and turgor pressure were then determined using the methods described by Johnson et al. (1984). These procedures were also conducted earlier during the experiment on an additional group of test plants set up for this purpose. This allowed leaf water status to be monitored on the day of RWA infestation and the day after _D_. _rapae_ were introduced without the necessity of destructively sampling test plants.

Qualitative evaluations of plant damage at harvest were made by visually rating the relative amounts of chlorosis due to RWA, and the extent of leaf rolling and plant stunting. Foliar chlorosis was rated on a 1 to 9 scale (Webster 1990) where 1 = healthy plants and 9 = chlorosis ≥ 85%; plants dead or beyond recovery. Leaf rolling was rated on a 1 to 3 scale where: 1 = no leaf rolling, 2 = one or more leaves conduplicately folded, and 3 = one or more leaves convolutely rolled. Plant stunting was rated by comparing the height of RWA infested plants with paired noninfested controls using a 1 to 5 scale based on 25% increments where: 1 = plant height equal to control, and 5

= plant height < 25% of control. Quantitative measurements of plant damage were obtained by counting the numbers of tillers and leaves, measuring total leaf length, and obtaining total leaf area using a Li-Cor Model 3100 area meter (Li-Cor, Inc., Lincoln, Nebr.). Also, plant shoots were separated from roots, oven dried at 65° C for 72 h, and weighed.

At plant harvest, all aphids and D. rapae mummies were removed from the plants and counted. Aphids were categorized into three groups: 1st and 2nd instar nymphs, 3rd and 4th instar nymphs, and apterous adults. Separate counts were made for each of these classes. D. rapae mummies were placed individually into gelatin capsules and observed daily for adult emergence. A subsample of 30 mummies for each parasitoid treatment was individually weighed. Upon emergence, adult D. rapae were sexed and the mummy width, adult head capsule width and femur length were measured using an ocular micrometer. Widths were also obtained for mummies from which adults never emerged. The parasitoid developmental period, % parasitization (no. mummies/no. RWA), % adult emergence and sex ratio were calculated. Calculations and data analyses were done with Statistical Analysis Systems (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Leaf turgor pressures that were measured at the time of aphid infestation, parasitoid introduction and at plant harvest are presented in Table 1. Clearly, a substantial level of drought stress was imposed by the drought treatment. Moreover, the reduction in leaf turgor in the droughted plants was exacerbated by RWA feeding. The RWA tolerant PI 372129 wheat was significantly more capable of maintaining its leaf turgor under droughted conditions when compared to 'TAM W-101'. Aphid feeding pressure alone was incapable of significantly reducing leaf turgor in the well-watered resistant plants, but did affect the susceptible. However, introduction of the parasitoid appeared to spare the 'TAM W-101', and leaf turgor did not differ from control plants. Overall, the drought stress treatment imposed by withholding water had an overriding effect on leaf turgor.

The qualitative ratings for plant stunting, leaf rolling, and leaf chlorosis due to RWA feeding is summarized in Table 2. Here again, the overriding influence of the drought imposed may be seen. It is important to note the sparing effect that occurred in the parasitoid treated resistant wheat; there was a significant reduction in the amount of leaf rolling and chlorosis when compared to RWA only treatments. No such effect was seen for the susceptible 'TAM W-101' entry. Plant stunting appeared to be the most sensitive parameter measured and did not differ between aphid only and aphid + parasitoid treatments.

Counts of tillers and leaves and measurements of total leaf length are given in Table 3. As expected, all droughted plants were severely affected and additional stress imposed by RWA had no significantly greater detrimental effect. Again, inclusion of the parasitoid in the well watered treatments spared those plants some of the damaging effects due to RWA, except for tiller production in the susceptible 'TAM W-101' entry.

Similar findings were exhibited by total leaf area and root and shoot biomass measurements (Table 4). Parasitoid presence did not significantly spare root biomass for the resistant wheat or shoot biomass for the susceptible wheat when compared to plants having aphids alone (well watered).

Mean number of aphids for each age class and total population for each treatment are shown in Table 5. In general, higher aphid populations were found on drought stressed plants. Overall, the parasitoid was capable of significantly lowering the total numbers of aphids found on the plants. The aphid population reductions were due to the ovipositional activities of one D. rapae female for a period restricted to twenty-four hours.

Parasitoid size and developmental period measurements are given in Table 6. A paired t-test was utilized to ascertain significant differences between the watered and droughted treatments for each parameter for each sex within each plant entry. The drought stressed resistant wheat treatment significantly lengthened the developmental period of both male and female parasitoids. In contrast, drought had no effect on development time of parasitoids on the susceptible wheat, 'TAM W-101'. The developmental delay on the resistant wheat, PI 372129, was over twice as long for females (1.8 d) than males (0.7 d). It is unknown whether this is due to some nutritional deficiency or some drought stress induced allelochemical (Price 1986). Under well watered conditions the parasitoid developmental period was similar for both PI 372129 and 'TAM W-101'. No differences were found between treatments for any of the size measurements taken from the parasitoid mummies or the adults.

Additional parasitoid parameters measured are given in Table 7. These include the parasitization rate, calculated as the percentage of mummies formed, based on the aphid population present at harvest, the mean mummy weight (n = 30/treatment), percentage emergence of adults from mummies, sex ratio, and the mean widths of mummies from which adults never emerged. Parasitoids placed on the drought stressed resistant wheat had a significantly lower parasitization rate than those on well watered plants. Observations seemed to indicate that this was because aphids on the resistant plants were less widely dispersed (less available) and more concentrated within the rolled leaves where seclusion may have limited parasitization, albeit these plants exhibited less tightly rolled leaves than 'TAM W-101'. There was also a significant male-biased sex ratio on the droughted PI 372129 when compared to well watered plants. Again, this effect was not seen on susceptible 'TAM W-101'. None of the additionally measured parameters differed significantly between treatments.

Three important measures of the capability of the parasitoid D. rapae to efficaciously suppress RWA populations were found to be detrimentally altered by drought stress in this experiment. These three measures were the parasitoid's developmental period, parasitization rate and sex ratio. In each case, the detrimental alteration occurred only on the RWA resistant wheat plants when subjected to severe drought stress. A short generation time enables a parasitoid to rapidly increase in numbers in response to the availability of aphid hosts. The ability to search effectively for aphid hosts, as measured by parasitization rate, is very important when hosts are at low density or are primarily present in secluded niches such as rolled leaves. Reductions in the production of female parasitoids can rapidly reduce the parasitoid's ability to reproduce and may lower fitness over the long term.

These results indicate that important interactions between plant resistance based on tolerance and drought stress may occur which may negatively impact biological control effectiveness. Plant structural effects, such as the induction of rolled leaves by RWA, and abiotic factors, such as drought, must be included when evaluating tritrophic interactions for their effects on insect pest management.

REFERENCES

Boethel, D.J. and R.D. Eikenbary, Eds. 1986. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Wiley, New York. 224 pp.

Burd, J.D., R.L. Burton and J.A. Webster. 1989. Plant damage caused by Russian wheat aphid feeding. Pages 144-145 in: Proc. Third Russian Wheat Aphid Conf., Albuquerque, New Mexico.

Burd, J.D., R.L. Burton and J.A. Webster. 1992. Evaluation of Russian wheat aphid damage on different host species with comparisons of damage ratings to quantitative plant measurements. J. Econ. Entomol. 85: (in press).

Burton, R.L. 1986. Effect of greenbug (Homoptera: Aphididae) damage on root and shoot biomass of wheat seedlings. J. Econ. Entomol. 79: 633-636.

Campbell, R.K., C.E. Salto, L.C. Sumner and R.D. Eikenbary. 1990. Tritrophic interactions between grains, the greenbug (Schizaphis graminum) and entomophaga. Pages 393-401 in: A. Szentesi and T. Jermy, Eds. Insects - Plants '89. (Symp. Biol. Hungary 39). Akadémiai Kiadó, Budapest.

Dorschner, K.W., R.C. Johnson, R.D. Eikenbary and J.D. Ryan. 1986. Insect-plant interactions: greenbugs (Homoptera: Aphididae) disrupt acclimation of winter wheat to drought stress. Environ. Entomol. 15: 118-121.

van Emden, H.F. and S.D. Wratten. 1991. Tri-trophic interactions involving plants in the biological control of aphids. Pages 29-43 in: D.C. Peters, J.A.Webster and C.S. Chlouber, Eds., Proceedings Aphid-Plant Interactions: Populations to Molecules, MP-132, Oklahoma Agricultural Experiment Station.

Hein, G., L. Brooks, G. Johnson, B. Massey, D. McBride, P. Morrison, J.F. Schultz, E. Spackman and F. Peairs. 1990. Economic impact of the Russian wheat aphid in the western United States: 1988-1989. Great Plains Agric. Council Pub. 10pp.

Johnson, R.C., H.T. Nguyen and L.I. Croy. 1984. Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. Crop Sci. 24: 957-962.

van Lenteren, J.C. 1991. Biological control in a tritrophic system approach. Pages 3-28 in: D.C. Peters, J.A.Webster and C.S. Chlouber, Eds., Proceedings Aphid-Plant Interactions: Populations to Molecules, MP-132, Oklahoma Agricultural Experiment Station.

Michels, G.J., Jr. and D.J. Undersander. 1986. Temporal and spatial distribution of the greenbug (Homoptera: Aphididae) on sorghum in relation to water stress. J. Econ. Entomol. 79: 1221-1225.

Price, P.W. 1986. Ecological aspects of host plant resistance and biological control: interactions among three trophic levels. Pages 11-30 in: Boethel, D.J. and R.D. Eikenbary, Eds. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Wiley, New York.

Quick, J.S. 1989. Developing RWA resistant wheat varieties. Page 14 in: Proc. Russian Wheat Aphid Conf., Albuquerque, New Mexico, Oct. 25-27, 1989. New Mexico State Univ.

Reed, D.K., J.A. Webster, B.G. Jones and J.D. Burd. 1991. Tritrophic relationships of Russian Wheat Aphid (Homoptera: Aphididae), a hymenopterous parasitoid (<u>Diaeretiella</u> <u>rapae</u> McIntosh), and resistant and susceptible small grains. Biological Control 1: 35-41.

Riedell, W.E. 1989. Effects of Russian wheat aphid infestation on barley plant response to drought stress. Physiol. Plant. 77: 587-592.

Sumner, L.C., J.T. Need, R.W. McNew, K.W. Dorschner, R.D. Eikenbary and R.C. Johnson. 1983. Response of <u>Schizaphis</u> <u>graminum</u> (Homoptera: Aphididae) to drought-stressed wheat, using polyethylene glycol as a matricum. Environ. Entomol. 12: 919-922.

Sumner, L.C., K.W. Dorschner, J.D. Ryan, R.D. Eikenbary, R.C. Johnson and R.W. McNew. 1986a. Reproduction of <u>Schizaphis</u> <u>graminum</u> (Homoptera: Aphididae) on resistant and susceptible wheat genotypes during simulated drought stress induced with polyethylene glycol. Environ. Entomol. 15: 756-762.

Sumner, L.C., R.D. Eikenbary and R.C. Johnson. 1986b. Survival and reproduction of *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae) on winter wheat during simulated drought stress. J. Kan. Entomol. Soc. 59: 561-563.

Webster, J.A. 1990. Resistance in triticale to the Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 83: 1091-1095.

Zadoks, J.C., T.T. Chang, and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14: 415-421.

TABLE 1

Plant Water Status During Experiment

	Leaf Turgor (MPa)		
Treatment	**Aphid Infestation**	**Parasitoid Infestation**	**Harvest**
PI 372I29	n = 5	n = 5	n = 10
Water			
Control	6.6 A	8.2 A	10.5 A
Aphid			8.35 A
Aphid + Parasitoid			9.89 A
Drought			
Control	4.5 B	7.3 A	4.3 B
Aphid			1.8 C
Aphid + Parasitoid			0.8 C
TAM W-101			
Water			
Control	6.2 AB	5.9 AB	9.2 A
Aphid			5.6 B
Aphid + Parasitoid			9.0 A
Drought			
Control	6.2 AB	3.8 B	2.4 C
Aphid			0.6 C
Aphid + Parasitoid			0.4 C

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 2

Visual Plant Damage Ratings at Termination of Experiment

	Ratings		
Treatment	**Stunting**	**Leaf Roll**	**Chlorosis**
PI 372I29			
Water			
Control	1.0 C	1.0 D	--
Aphid	2.2 B	2.2 C	2.8 A
Aphid + Parasitoid	2.2 B	1.0 D	2.2 B
Drought			
Control	3.0 A	3.0 A	--
Aphid	3.1 A	2.5 B	2.4 AB
Aphid + Parasitoid	3.2 A	2.8 A	2.8 A
TAM W-101			
Water			
Control	1.0 C	1.0 C	--
Aphid	1.5 B	2.4 B	2.5 B
Aphid + Parasitoid	1.2 BC	2.3 B	2.4 B
Drought			
Control	3.4 A	3.0 A	--
Aphid	3.2 A	3.0 A	3.4 A
Aphid + Parasitoid	3.1 A	3.0 A	3.1 A

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 3

Plant Characteristics at Termination of Experiment

	Plant Measurements		
Treatment	**Tillers**	**Leaves**	**Leaf Length (cm)**
PI 372129			
Water			
Control	3.5 A	14.6 A	366.7 A
Aphid	2.7 B	10.8 C	227.4 C
Aphid + Parasitoid	3.5 A	12.6 B	267.9 B
Drought			
Control	1.7 C	7.2 D	125.2 D
Aphid	1.5 C	6.6 D	114.7 D
Aphid + Parasitoid	1.6 C	6.5 D	109.4 D
TAM W-101			
Water			
Control	3.9 A	18.0 A	348.9 A
Aphid	3.2 B	12.9 C	255.4 C
Aphid + Parasitoid	2.7 B	14.5 B	283.9 B
Drought			
Control	1.8 C	8.2 D	116.8 D
Aphid	1.5 C	7.0 D	110.6 D
Aphid + Parasitoid	1.9 C	6.9 D	103.2 D

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 4

Additional Plant Measurements at Termination of Experiment

Treatment	Plant Measurements		
	Leaf Area (cm^2)	Shoot Wt (g)	Root Wt (g)
PI 372129			
Water			
Control	123.7 A	0.754 A	0.385 A
Aphid	61.2 C	0.511 C	0.271 BC
Aphid + Parasitoid	83.6 B	0.623 B	0.290 B
Drought			
Control	23.1 D	0.450 D	0.233 C
Aphid	20.9 D	0.322 D	0.201 D
Aphid + Parasitoid	18.3 D	0.303 D	0.201 D
TAM W-101			
Water			
Control	125.8 A	0.810 A	0.437 A
Aphid	83.9 C	0.674 B	0.244 C
Aphid + Parasitoid	94.4 B	0.673 B	0.306 B
Drought			
Control	17.5 D	0.463 C	0.303 B
Aphid	20.1 D	0.399 D	0.245 C
Aphid + Parasitoid	17.2 D	0.419 CD	0.261 BC

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 5

Russian Wheat Aphid Populations Per Plant at Termination of Experiment

	Mean Aphid Populations			
Treatment	**1st + 2nd Instar**	**3rd + 4th Instar**	**Adult**	**Total**
PI 372129				
Water				
Aphid	85.6 BC	68.0 AB	50.9 AB	206.1 ABC
Aphid + Parasitoid	84.6 BC	47.5 AB	51.3 AB	184.2 ABC
Drought				
Aphid	170.7 A	103.6 A	66.2 A	341.8 A
Aphid + Parasitoid	65.7 C	55.0 AB	38.9 AB	161.2 C
TAM W-101				
Water				
Aphid	70.4 BC	50.5 AB	45.8 AB	166.9 BC
Aphid + Parasitoid	24.3 C	32.6 B	18.7 B	75.8 C
Drought				
Aphid	147.8 AB	108.4 A	79.0 A	335.4 AB
Aphid + Parasitoid	56.4 C	64.6 AB	50.9 AB	172.6 ABC

Means in a column followed by different letters are significantly different (*P* < 0.05; Tukey's HSD test).

TABLE 6

Diaeretiella rapae Development and Size Measurements

	Mean Parasitoid Growth Measurements							
Treatment	**Egg to Adult (days)**		**Mummy Width (μm)**		**Head Width (μm)**		**Femur Length (μm)**	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
PI 372129 **Water**	14.6 B	15.2 B	819.7 A	807.2 A	352.3 A	349.0 A	284.1 A	284.6 A
Drought	15.5 A	17.0 A	825.2 A	790.0 A	345.5 A	336.7 A	281.8 A	296.7 A
TAM W-101 **Water**	14.7 A	15.2 A	823.4 A	815.2 A	347.8 A	345.5 A	285.2 A	288.5 A
Drought	14.8 A	15.5 A	834.8 A	798.3 A	339.3 A	345.6 A	286.0 A	289.4 A

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 7

Additional *Diaeretiella rapae* Parameters Measured

	Measured Parameters				
Treatment	**Parasitization (%)**	**Mummy Wt (μg)**	**Emergence (%)**	**Sex Ratio (% female)**	**Dead Mummy Width (μm)**
PI 372129 **Water**	**6.4 A**	**157.5 A**	**70.6 A**	**54.7 A**	**767.5 A**
Drought	**1.3 B**	**171.5 A**	**70.7 A**	**20.7 B**	**748.3 A**
TAM W-101 **Water**	**7.8 A**	**159.0 A**	**62.9 A**	**58.9 A**	**768.8 A**
Drought	**7.8 A**	**165.6 A**	**65.7 A**	**54.5 A**	**803.4 A**

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

PART IV

RUSSIAN WHEAT APHID AND DROUGHT STRESSES IN BARLEY: TRITROPHIC INTERACTIONS WITH PLANT RESISTANCE AND A PARASITOID

INTRODUCTION

The Russian Wheat Aphid (RWA), *Diuraphis noxia* (Mordvilko), has become a serious pest of grains in North America (Hein et al. 1990). Heavily infested plants exhibit striking damage symptoms including prostrate growth, interveinal bleaching, and diminished leaf expansion caused by impaired cell wall extensibility (Burd et al. 1989, 1992). Such unexpanded (rolled) leaves serve as refugia for the aphid colonies thus limiting effective search and attack by aphid parasitoids.

Interest in the interactions of host plant resistance and biological control, ie. tritrophic interactions, has been expanding rapidly in recent years. This has been true for both insect pests in general (Boethel and Eikenbary 1986) and for aphids in particular (van Emden and Wratten 1991, van Lenteren 1991). Initial investigations on tritrophic interactions with RWA were included in a study focused primarily on the greenbug, *Schizaphis graminum* (Rondani) (Campbell et al. 1990). However, because the parasitoid used was a greenbug adapted strain of *Lysiphlebus testaceipes* (Cresson) it proved incapable of effectively parasitizing the RWA and the greenbug resistant wheat (*Triticum aestivum* L.) used exhibited no significant resistance to RWA. More recently, Reed et al. (1991) found that an antibiotic RWA resistant triticale (x*Triticosecale*) (PI 386148) detrimentally affected the growth and reproduction of both the RWA and one of its parasitoids, *Diaeretiella rapae* McIntosh. They also showed that a tolerant RWA resistant wheat (PI 372129) was beneficial for parasitoid action because the extent of leaf rolling was substantially reduced.

Drought and aphid infestations of cereal crops often occur together or sequentially during the growing season, yet few studies have investigated interactions of grain aphids and drought stressed grains. Sumner et al. (1983) found that wheat stressed with polyethylene glycol (PEG) reduced the fecundity and longevity of greenbug biotype C (GBC) when the plants were osmotically stressed to below a critical threshold. A subsequent study (Sumner et al. 1986a) analyzed the response of GBC to controlled levels of PEG induced osmotic stress on GBC resistant (OK 80268) and susceptible (cv. Sturdy) wheat. They reported that greenbug longevity (days to death) was not altered by the host plant but was significantly decreased by the PEG induced water stress. However, GBC fecundity was highly dependent upon the host plant, and was significantly reduced on the GBC resistant cultivar. Moreover, water stress reduced GBC fecundity on the susceptible wheat to levels equal to or lower than those for the non-stressed resistant entry. The simulated stress also significantly reduced GBC fecundity on the resistant wheat. Similar studies on wheat using the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), showed that fecundity, longevity and the reproductive period of the aphid declined linearly with increasing osmotic stress levels (Sumner et al. 1986b). Michels and Undersander (1986) found that greenbug reproduction was reduced on water stressed field grown grain sorghum, (*Sorghum bicolor* (L.) Moench. Similar results were obtained by Dorschner et al. (1986) in growth chamber experiments where greenbug densities (number of greenbug per mg shoot dry weight) were greater on drought-stressed wheat plants. Riedell (1989) found that RWA infestation of barley, (*Hordeum vulgare* L.), plants limits the plants' ability to adjust osmotically to subsequent drought stress. In particular, plants previously infested with RWA have a decreased ability to adjust osmotically and thereby maintain adequate leaf relative water content in response to drought stress.

Although some progress has been made in understanding the effects of water deficits on grains and their aphids, there still remains a great void in determining how cereal aphids and drought stresses interact with different grain species. Virtually nothing is known of the interactions of drought, RWA, plant resistance and biological control. This study was undertaken to investigate these interactions using seedlings of a susceptible barley cultivar ('Wintermalt') (Webster et al. 1987), a barley line from Afghanistan which exhibited significant RWA resistance in a U. S. screening trial (PI 366450) (Webster et al. 1991), RWA and a Russian strain of the parasitoid D. rapae.

MATERIALS AND METHODS

The experiment was conducted in a greenhouse during September and October with supplemental metal halide lighting to provide a 14 h photophase. Temperatures were controlled at 22 ± 4° C. Individual plants were grown from pre-germinated seed in a fritted clay medium (Absorb-N-Dry, Balcones Minerals, Flatonia, Tex.) in cone-tainers (Supercell Cone-Tainer, Ray Leach Cone-Tainer Nursery, Canby, Ore.) (Burton 1986). Plants were infested with 15 mature apterous RWA at the 3-leaf stage (GS 13, Zadoks et al. 1974) and both infested and control plants were caged with ventilated clear plastic cages. Main effect treatments included combinations of plant resistance, drought, RWA infestation, and D. rapae and were replicated 15 times. Plants subjected to drought stress treatments received only minimal amounts of maintenance water while non-stressed plants were regularly watered to capacity. All plants were fertilized biweekly with Peters' Complete Peat-Lite Special (analysis 15-16-17) (Peters Fertilizer Products, Fogelsville, Penn.). Those treatments receiving parasitoids received one mating pair of D. rapae 10 d after aphid infestation. The parasitoids were removed after 24 h. The experiment was continued for an additional 8 d to provide a sufficient time for the formation of the F1 parasitoid mummies. Subsequently, the experiment was terminated and a number of plant, aphid and parasitoid parameters measured.

Leaf water status of ten replicates from each treatment combination was measured by excising 0.24 cm^2 leaf discs from 3 cm above the base of the second fully expanded leaf on the main stem of each plant using leaf-cutter psychrometers (J.R.D. Merrill Specialty Equipment, Logan, Utah). Water potential, osmotic potential, and turgor pressure were then determined using the methods described by Johnson et al. (1984). These procedures were also conducted earlier during the experiment on an additional group of test plants set up for this purpose. This allowed leaf water status to be monitored on the day of RWA infestation and the day after D. rapae were introduced without the necessity of destructively sampling test plants.

Qualitative evaluations of plant damage at harvest were made by visually rating the relative amounts of chlorosis due to RWA, and the extent of leaf rolling and plant stunting. Foliar chlorosis was rated on a 1 to 9 scale (Webster 1990) where 1 = healthy plants and 9 = chlorosis ≥ 85%; plants dead or beyond recovery. Leaf rolling was rated on a 1 to 3 scale where: 1 = no leaf rolling, 2 = one or more leaves conduplicately folded, and 3 = one or more leaves convolutely rolled. Plant stunting was rated by comparing the height of RWA infested plants with paired noninfested controls using a 1 to 5 scale based on 25% increments where: 1 = plant height equal to control, and 5

= plant height < 25% of control. Quantitative measurements of plant damage were obtained by counting the numbers of tillers and leaves, measuring total leaf length, and obtaining total leaf area using a Li-Cor Model 3100 area meter (Li-Cor, Inc., Lincoln, Nebr.). Also, plant shoots were separated from roots, oven dried at 65° C for 72 h, and weighed.

At plant harvest, all aphids and _D_. _rapae_ mummies were removed from the plants and counted. Aphids were categorized into four groups: 1st and 2nd instar nymphs, 3rd and 4th instar nymphs, apterous adults and alate adults. Separate counts were made for each of these classes. _D_. _rapae_ mummies were placed individually into gelatin capsules and observed daily for adult emergence. A subsample of 75 mummies for each parasitoid treatment was individually weighed. Upon emergence, adult _D_. _rapae_ were sexed and the mummy width, adult head capsule width and femur length were measured using an ocular micrometer. Widths were also obtained for mummies from which adults never emerged. The parasitoid developmental period, % parasitization (no. mummies/no. RWA), % adult emergence and sex ratio were calculated. Calculations and data analyses were done with Statistical Analysis Systems (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Leaf turgor pressures that were measured at the time of aphid infestation, parasitoid introduction and at plant harvest are presented in Table 1. Clearly, a substantial level of drought stress was imposed by the drought treatment. Moreover, the reduction in leaf turgor in the droughted plants was exacerbated by RWA feeding. The RWA tolerant PI 366450 barley was not significantly more capable of maintaining its leaf turgor under droughted conditions when compared to 'Wintermalt'. Aphid feeding pressure alone was capable of significantly reducing turgor in both plant entries. However, introduction of the parasitoid partially spared well-watered treatments of both plant entries, and reduction of turgor was intermediate. Overall, the drought stress treatment imposed by withholding water had an overriding effect on the aphid - parasitoid interaction in terms of turgor maintenance.

Table 2 summarizes the qualitative ratings for plant stunting, extent of leaf rolling, and leaf chlorosis due to RWA feeding. For the RWA tolerant PI 366450 drought had an overriding effect upon plant stunting with aphid feeding increasing stunting only on well watered plants and then only slightly if parasitoids were present. PI 366450 resisted RWA feeding induced reduction of leaf expansion (leaf rolling) but was less able to do so under drought. Leaf chlorosis was also increased under drought. In general, the parasitoids' presence was unable to spare PI 366450 of RWA caused detrimental effects. Susceptible 'Wintermalt' was greatly stunted by drought by RWA feeding. Similar reductions occurred for leaf rolling and chlorosis.

However, the parasitoid was able to spare these plants some stunting and chlorosis when both stresses were present.

The number of tillers and leaves and measurements of total leaf length are given in Table 3. As expected, the growth response of the droughted plants were severely affected. Significantly greater reductions in growth were observed when aphid feeding occurred on 'Wintermalt'. Aphid feeding in the well-watered treatments reduced numbers of leaves and leaf lengths in PI 366450 and all three parameters in 'Wintermalt'. Inclusion of the parasitoid spared loss in leaf production on Wintermalt.

Similar findings were exhibited for total leaf area and root and shoot biomass measurements (Table 4), although the tolerant barley suffered loss in leaf area due to aphid feeding alone. 'Wintermalt' maintained shoot biomass under drought but was severely affected when RWA were also present. Parasitoid presence lessened the amount of biomass reduction in 'Wintermalt'.

Mean number of aphids for each age class and total population for each treatment are shown in Table 5. Few differences among treatment combinations are apparent. The parasitoid usually significantly lowered the total number of aphids on the plants. This population reduction is due to the ovipositional activities of one _D_. _rapae_ female for a period of twenty-four hours.

Size and developmental period measurements for the parasitoid are given in Table 6. A paired t-test (LSD) was utilized to ascertain significant differences for each parameter between the watered and droughted treatments for each sex within each plant entry. Interestingly, both drought stressed barleys significantly shortened the developmental period of male and female parasitoids. Sizes of parasitoid mummies were also reduced under drought. On 'Wintermalt', drought caused decreased head widths for adult female parasitoids and decreased femur lengths for males. Yet, femur lengths were increased on droughted PI 366450.

Additional parasitoid parameters measured are given in Table 7. These include the parasitization rate calculated as the percentage of mummies formed based on the aphid population present at harvest, the mean mummy weight (n = 75/treatment), percentage emergence of adults from mummies, sex ratio, and the mean widths of mummies from which adults never emerged. Parasitoids placed on the drought stressed resistant barley had a significantly lower parasitization rate than those on well-watered plants. Observations seemed to indicate that this was because aphids on these plants were less widely dispersed (less available) and more concentrated within the new rolled leaf areas where seclusion limited parasitization even though overall these plants exhibited less tightly rolled leaves than 'Wintermalt'. The 'Wintermalt' had tightly rolled leaves on both watered and droughted plants but the RWA population may not have been as concentrated within these rolled areas. Mummy weights were found to be significantly reduced on the resistant barley compared to the susceptible, particularly under drought. Emergence percentage was highest on droughted PI 366450 and lowest on watered 'Wintermalt'. Perhaps, seclusion of RWA limits parasitization but increases protection of those mummies formed, thus improving successful emergence of parasitoid adults from those aphids which were parasitized. There were few other differences although even dead (never emerged) mummies tended to be smaller on drought stressed plants.

Three important characteristics of the parasitoid D. rapae which determine its ability to rapidly reproduce and efficaciously suppress RWA populations were influenced by either resistant plants or the drought stress imposed. These include alterations in developmental periods, mummy and adult sizes and parasitization rates. These results indicate that important interactions between plant resistance based on tolerance and drought stress may occur which may impact biological control effectiveness. Plant structural effects, such as the induction of rolled leaves by RWA, and abiotic factors, such as drought, must be included when evaluating tritrophic interactions for their effects on insect pest management.

REFERENCES

Boethel, D.J. and R.D. Eikenbary, Eds. 1986. Interactions of Plant Resistance and Parasitoids and Predators of Insects. Wiley, New York. 224 pp.

Burd, J.D., R.L. Burton and J.A. Webster. 1989. Plant damage caused by Russian wheat aphid feeding. Pages 144-145 in: Proc. Third Russian Wheat Aphid Conf., Albuquerque, New Mexico.

Burd, J.D., R.L. Burton and J.A. Webster. 1992. Evaluation of Russian wheat aphid damage on different host species with comparisons of damage ratings to quantitative plant measurements. J. Econ. Entomol. 85: (in press).

Burton, R.L. 1986. Effect of greenbug (Homoptera: Aphididae) damage on root and shoot biomass of wheat seedlings. J. Econ. Entomol. 79: 633-636.

Campbell, R.K., C.E. Salto, L.C. Sumner and R.D. Eikenbary. 1990. Tritrophic interactions between grains, the greenbug (Schizaphis graminum) and entomophaga. Pages 393-401 in: A. Szentesi and T. Jermy, Eds. Insects - Plants '89. (Symp. Biol. Hungary 39). Akadémiai Kiadó, Budapest.

Dorschner, K.W., R.C. Johnson, R.D. Eikenbary and J.D. Ryan. 1986. Insect-plant interactions: greenbugs (Homoptera: Aphididae) disrupt acclimation of winter wheat to drought stress. Environ. Entomol. 15: 118-121.

van Emden, H.F. and S.D. Wratten. 1991. Tri-trophic interactions involving plants in the biological control of aphids. Pages 29-43 in: D.C. Peters, J.A.Webster and C.S. Chlouber, Eds., Proceedings Aphid-Plant Interactions: Populations to Molecules, MP-132, Oklahoma Agricultural Experiment Station.

Hein, G., L. Brooks, G. Johnson, B. Massey, D. McBride, P. Morrison, J.F. Schultz, E. Spackman and F. Peairs. 1990. Economic impact of the Russian wheat aphid in the western United States: 1988-1989. Great Plains Agric. Council Pub. 10pp.

Johnson, R.C., H.T. Nguyen and L.I. Croy. 1984. Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. Crop Sci. 24: 957-962.

van Lenteren, J.C. 1991. Biological control in a tritrophic system approach. Pages 3-28 in: D.C. Peters, J.A.Webster and C.S. Chlouber, Eds., Proceedings Aphid-Plant Interactions: Populations to Molecules, MP-132, Oklahoma Agricultural Experiment Station.

Michels, G.J., Jr. and D.J. Undersander. 1986. Temporal and spatial distribution of the greenbug (Homoptera: Aphididae) on sorghum in relation to water stress. J. Econ. Entomol. 79: 1221-1225.

Reed, D.K., J.A. Webster, B.G. Jones and J.D. Burd. 1991. Tritrophic relationships of Russian Wheat Aphid (Homoptera: Aphididae), a hymenopterous parasitoid (Diaeretiella rapae McIntosh), and resistant and susceptible small grains. Biological Control 1: 35-41.

Riedell, W.E. 1989. Effects of Russian wheat aphid infestation on barley plant response to drought stress. Physiol. Plant. 77: 587-592.

Sumner, L.C., J.T. Need, R.W. McNew, K.W. Dorschner, R.D. Eikenbary and R.C. Johnson. 1983. Response of Schizaphis graminum (Homoptera: Aphididae) to drought-stressed wheat, using polyethylene glycol as a matricum. Environ. Entomol. 12: 919-922.

Sumner, L.C., K.W. Dorschner, J.D. Ryan, R.D. Eikenbary, R.C. Johnson and R.W. McNew. 1986a. Reproduction of Schizaphis graminum (Homoptera: Aphididae) on resistant and susceptible wheat genotypes during simulated drought stress induced with polyethylene glycol. Environ. Entomol. 15: 756-762.

Sumner, L.C., R.D. Eikenbary and R.C. Johnson. 1986b. Survival and reproduction of Rhopalosiphum maidis (Fitch) (Homoptera: Aphididae) on winter wheat during simulated drought stress. J. Kan. Entomol. Soc. 59: 561-563.

Webster, J.A., K.J. Starks and R.L. Burton. 1987. Plant resistance studies with Diuraphis noxia (Homoptera: Aphididae), a new United States wheat pest. J. Econ. Entomol. 80: 944-949.

Webster, J.A. 1990. Resistance in triticale to the Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 83: 1091-1095.

Webster, J.A., C.A. Baker and D.R. Porter. 1991. Detection and mechanisms of Russian wheat aphid (Homoptera: Aphididae) resistance in barley. J. Econ. Entomol. 84: 669-673.

Zadoks, J.C., T.T. Chang, and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14: 415-421.

TABLE 1

Plant Water Status During Experiment

	Leaf Turgor (MPa)		
Treatment	**Aphid Infestation**	**Parasitoid Infestation**	**Harvest**
PI 366450	n = 5	n = 5	n = 10
Water			
Control	14.3 A	7.3 A	10.5 A
Aphid			4.9 C
Aphid + Parasitoid			6.2 B
Drought			
Control	7.0 B	4.1 B	1.7 D
Aphid			1.2 D
Aphid + Parasitoid			1.9 D
WINTERMALT			
Water			
Control	13.3 A	7.9 A	9.4 A
Aphid			2.9 C
Aphid + Parasitoid			5.3 B
Drought			
Control	6.9 B	4.0 B	2.4 CD
Aphid			1.7 D
Aphid + Parasitoid			1.9 D

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 2

Visual Plant Damage Ratings at Termination of Experiment

Treatment	Ratings Stunting	 Leaf Roll	 Chlorosis
PI 366450			
Water			
Control	1.0 C	1.0 C	--
Aphid	1.4 B	1.0 C	2.5 B
Aphid + Parasitoid	1.1 BC	1.0 C	2.1 B
Drought			
Control	3.3 A	1.3 B	--
Aphid	3.2 A	1.6 A	3.4 A
Aphid + Parasitoid	2.9 A	1.5 AB	3.5 A
WINTERMALT			
Water			
Control	1.0 D	1.0 C	--
Aphid	3.4 B	3.0 A	5.0 BC
Aphid + Parasitoid	3.1 B	3.0 A	4.5 C
Drought			
Control	2.5 C	2.0 B	--
Aphid	4.1 A	3.0 A	6.9 A
Aphid + Parasitoid	3.5 B	3.0 A	5.2 B

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 3

Plant Characteristics at Termination of Experiment

	Plant Measurements		
Treatment	**Tillers**	**Leaves**	**Leaf Length (cm)**
PI 366450			
Water			
Control	2.4 A	13.1 A	293.5 A
Aphid	2.0 A	10.0 B	218.9 B
Aphid + Parasitoid	2.2 A	10.0 B	203.4 B
Drought			
Control	0.8 B	5.3 C	74.4 C
Aphid	0.0 C	4.4 C	38.3 C
Aphid + Parasitoid	0.3 C	4.7 C	43.2 C
WINTERMALT			
Water			
Control	3.3 A	17.4 A	388.5 A
Aphid	2.2 B	9.5 B	128.2 B
Aphid + Parasitoid	1.8 B	9.2 B	134.4 B
Drought			
Control	1.2 C	7.7 C	120.7 BC
Aphid	0.9 C	5.9 D	65.8 D
Aphid + Parasitoid	0.9 C	7.7 C	90.0 CD

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 4

Additional Plant Measurements at Termination of Experiment

	Plant Measurements		
Treatment	**Leaf Area (cm^2)**	**Shoot Wt (g)**	**Root Wt (g)**
PI 366450			
Water			
Control	195.0 A	0.646 A	0.356 A
Aphid	135.3 B	0.409 B	0.227 B
Aphid + Parasitoid	139.9 B	0.405 B	0.227 B
Drought			
Control	34.0 C	0.231 C	0.152 C
Aphid	21.8 C	0.110 D	0.140 C
Aphid + Parasitoid	26.5 C	0.123 D	0.082 D
WINTERMALT			
Water			
Control	254.9 A	0.789 A	0.266 A
Aphid	54.8 B	0.238 CD	0.141 C
Aphid + Parasitoid	53.1 B	0.242 C	0.106 D
Drought			
Control	35.8 C	0.365 B	0.191 B
Aphid	22.3 C	0.091 E	0.109 CD
Aphid + Parasitoid	29.3 C	0.171 D	0.129 CD

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 5

Russian Wheat Aphid Populations Per Plant at Termination of Experiment

	Mean Aphid Populations				
Treatment	**Small**	**Large**	**Apterae**	**Alatae**	**Total**
PI 366450					
Water					
Aphid	870.0 AB	358.9 ABC	41.9 AB	37.7 BC	1308.5 AB
Aphid + Parasitoid	565.1 BC	255.3 BCD	37.1 ABC	24.4 C	881.9 CD
Drought					
Aphid	845.9 AB	229.4 CD	56.3 A	65.7 A	1197.4 ABC
Aphid + Parasitoid	600.3 BC	362.9 AB	35.1 ABC	30.7 BC	1029.0 BCD
WINTERMALT					
Water					
Aphid	961.4 A	469.2 A	15.9 C	47.0 AB	1493.5 A
Aphid + Parasitoid	631.8 ABC	318.7 BC	35.5 ABC	44.4 ABC	1030.4 BCD
Drought					
Aphid	971.6 A	233.1 BCD	29.5 BC	47.0 AB	1281.3 AB
Aphid + Parasitoid	437.1 C	167.5 D	26.1 BC	30.5 BC	661.3 D

Means in a column followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 6

Diaeretiella rapae Development and Size Measurements

	Mean Parasitoid Growth Measurements							
Treatment	**Egg to Adult (days)**		**Mummy Width (μm)**		**Head Width (μm)**		**Femur Length (μm)**	
	Male	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**
PI 366450 **Water**	**11.7 A**	**12.2 A**	**956.4 A**	**934.3 A**	**336.4 A**	**338.1 A**	**323.1 B**	**317.0 B**
Drought	**11.3 B**	**11.8 B**	**907.8 B**	**920.6 A**	**335.5 A**	**337.4 A**	**331.7 A**	**322.7 A**
WINTERMALT **Water**	**11.2 A**	**11.8 A**	**943.2 A**	**919.2 A**	**350.5 A**	**345.0 A**	**333.6 A**	**321.0 A**
Drought	**11.0 B**	**11.5 B**	**918.4 B**	**887.0 B**	**350.0 A**	**338.7 B**	**326.8 B**	**320.0 A**

Means in a column for each plant entry followed by different letters are significantly different ($P < 0.05$; LSD test).

TABLE 7

Additional *Diaeretiella rapae* Parameters Measured

	Measured Parameters				
Treatment	**Parasitization (%)**	**Mummy Wt (μg)**	**Emergence (%)**	**Sex Ratio (% female)**	**Dead Mummy Width (μm)**
PI 366450 **Water**	**10.9 A**	**168.8 AB**	**70.4 AB**	**57.7 A**	**891.7 A**
Drought	**3.9 B**	**158.5 B**	**78.2 A**	**59.6 A**	**840.9 BC**
WINTERMALT **Water**	**9.3 AB**	**193.1 A**	**61.9 B**	**64.2 A**	**867.5 AB**
Drought	**8.4 AB**	**189.4 A**	**71.4 AB**	**53.8 A**	**827.4 C**

Means in a column followed by different letters are significantly different ($P < 0.05$; Tukey's HSD test).

PART V

CONCLUSIONS

CONCLUSIONS

The results of the experimentation reported on in Part II illustrate that host plant resistance and biological control can be complementary in extending plant survival and reducing plant damage. Plant resistance may slow aphid population growth (antibiosis) or limit plant damage (tolerance). Either mechanism could slow the accumulation of plant damage during the 'critical lag period' prior the movement of aphid parasitoids into the grain crop canopy. Certainly, additional research should be conducted to determine the effects of lag periods other than 8 d as reported here, and other temperature regimes and resistant cultivars. Recent field collections of L. testaceipes indicate that this ubiquitous parasitoid has adapted to the Russian wheat aphid as a host.

The experiments of Parts III and IV were conducted in a very similar manner which allows general comparisons between the two host plants, wheat and barley. In general, barley is a much better host plant for the Russian wheat aphid than is wheat as evidenced by the much greater population growth on barley. This occurred even though a smaller initial infestation was used in the barley experiment. A great deal of drought stress was imposed in these experiments and it often exacerbated plant responses to RWA feeding. For example, the resistant PI 366450 barley could resist leaf rolling when well-watered but was less able to do so under drought. The most interesting general trend evident in the drought experiments was the influence of drought in magnifying any effects that resistant plants had on the third trophic level, the aphid parasitoids. Well-watered resistant plants did not generally have any detrimental effects on parasitoids, possibly because the type of resistance observed was tolerance. However, plants that are water stressed may become more antibiotic. This would certainly be an avenue for future research to take.

The effective combination of host plant resistance and biological control will require tritrophic level interaction research for each plant-pest-natural enemy system of interest. Abiotic stresses such as drought can drastically alter important specifics of such interactions. It will remain important that those who wish to develop pest management systems keep in mind that attempting to apply generalizations from one crop system to another will be fraught with pitfalls.

2

VITA

Russell Kenneth Campbell

Candidate for the Degree of

Doctor of Philosophy

Thesis: APHID AND DROUGHT STRESSES IN SMALL GRAINS: TRITROPHIC INTERACTIONS WITH APHID PARASITOIDS AND PLANT RESISTANCE

Major Field: Entomology

Biographical:

Personal Data: Born in Enid, Oklahoma, August 30, 1954, the son of Kenneth and Lucy T. Campbell.

Education: Graduated valedictorian from Kremlin High School in Kremlin, Oklahoma, May, 1972; attended Phillips University in Enid, Oklahoma, from June, 1972 to December, 1973; received Bachelor of Science degree in Entomology from Oklahoma State University in Stillwater, Oklahoma, May, 1977; attended Oklahoma State University in Stillwater, Oklahoma, from September, 1977 to July, 1979; attended Cornell University in Ithaca, New York from January, 1980 to December, 1980; attended Oklahoma State University from January, 1982 to May, 1984; received Master of Science degree in Entomology from Oklahoma State University in Stillwater, Oklahoma, May, 1987; completed the requirements for the Doctor of Philosophy degree in Entomology at Oklahoma State University, May, 1992.

Professional Experience: Student Assistant, Departments of Botany and Plant Pathology and Entomology, Oklahoma State University, in Stillwater, Oklahoma, October, 1974 to June, 1976; Laboratory Helper, Department of Entomology, Oklahoma State University, in Stillwater, Oklahoma, June, 1976 to May, 1977; Laboratory and Field Assistant, Department of Entomology, Oklahoma State University, in Stillwater, Oklahoma, May, 1977 to September, 1977; Laboratory Technologist I, Department of Entomology, Oklahoma State University, in Stillwater, Oklahoma, September 1977 to September, 1979; Research Assistant I, Boyce Thompson Institute for Plant Research, in Ithaca, New York, September, 1979 to January, 1981; Graduate Research Assistant, Department of Entomology, Oklahoma State University, in Stillwater, Oklahoma, January, 1982 to May, 1984; Senior Agriculturist, Department of Entomology, Oklahoma State University, in Stillwater, Oklahoma, April, 1986 to present.

Professional Organizations: Entomological Society of America, International Organization for Biological Control of Noxious Animals and Plants, Sigma Xi, Phi Kappa Phi Honor Society