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The Effects of Planting Date and Varietal Susceptibility of *Gossypium hirsutum* L. on Thrips

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THE EFFECTS OF PLANTING DATE AND VARIETAL SUSCEPTIBILITY
OF *GOSSYPIUM HIRSTUTUM* L. ON THRIPS

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Entomology

by
Cody D. Kerns
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ABSTRACT

Thysanoptera (Haliday) or thrips, are minute, polyphagous insects known globally for their role as crop pests. One species important economically to South Carolina and the southeastern United States is the tobacco thrips, *Frankliniella fusca* (Hinds). This species is the most predictable pest of upland cotton, *Gossypium hirsutum* (L.). Thrips are particularly damaging to cotton when they infest seedling cotton. In some years, tobacco thrips are recorded as the most detrimental pest of cotton in terms yield loss. Yield loss from tobacco thrips infestations varies widely between years and even within the same year. By analyzing agricultural control practices, an accurate window of infestation can be found. Understanding when tobacco thrips infestations occur gives farmers an idea of the risk they may incur for a given planting date. Cotton farmers need more accurate risk projections for tobacco thrips infestations to combat infesting thrips populations with reduced sensitivity to neonicotinoid class insecticides. Cultural control practices are needed to help mitigate tobacco thrips management problems associated with reduced sensitivities to chemicals.

Two potential cultural control practices for tobacco thrips are planting date and host plant resistance. Planting date and choice of variety mitigate injury from *F. fusca* infestations in cotton. A planting date study was conducted in Blackville, South Carolina, using a mid-full maturing variety in 2015, an early maturing variety in 2016, and both an early maturing and a mid-full maturing variety in 2017. In every year, cotton planted after mid-May suffered significantly lower thrips densities and subsequent injury from thrips. A variety study was also conducted in 2016 and 2017 in seven sites across the Southern

United States with varieties PHY 312, PHY 333, PHY 444, PHY 499, DP 1646, DP 1410, DP 1538, ST 4747, ST 4946, ST 6182, and FM1900. ST 4946, a variety with a consistently larger seed size, generally had larger dry weights and less injury than other varieties despite having a similar amount of thrips infesting it. A significant correlation was found in the study between cotton plant seed size and weight compared to cotton plant dry weight and cotton plant height. The information reported in these studies can aid cotton farmers from a risk management perspective to make the best decision for their thrips prone fieldsmanage thrips in cotton.

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CHAPTER ONE

LITERATURE REVIEW

Introduction

Thrips are minute insects, usually one millimeter long or less, but reaching up to four millimeters in certain species. They are found in macropterous, brachypterous, or apterous forms. When they are winged, the wings appear as fringed hairs. Thrips are hemimetabolous. They do not have a true pupae, but they do enter into a resting stage of life where movement is possible, but limited, and in which the organism does not feed. Thrips can feed on a variety of hosts. In general, thrips feed on plant material, other insects, pollen, and fungi. Thrips that feed on plant material can often be agricultural pests. One of the crops on which thrips are pests is cotton, *Gossypium hirsutum* (L.), and the predominant species of thrips infesting seedling cotton in the southeastern USA is tobacco thrips, *Frankliniella fusca*. Recent research on seedling cotton in 2014 and 2015 showed that, on average, tobacco thrips outnumber other species of thrips seven to one in Georgia, Alabama, South Carolina, and Virginia (Reay-Jones et al. 2017). Because of the potential yield losses (Sadras and Wilson 1998) and delays in maturity/harvest (Reay-Jones et al. 2017), thrips can be economic factors that require control in cotton. Therefore, at- and/or post-plant insecticides are used for chemical control of thrips in the crop, but some species of thrips, including tobacco thrips (Huseth et al. 2016) have become tolerant to commonly used insecticides. In addition to chemical control, other methods of managing thrips in cotton should be developed and implemented. Cultural control methods using planting date and host plant resistance are potential options for

mitigating injury from and losses to thrips in the crop. Understanding the impact of agricultural control on populations of *F. fusca* is critical to understanding how to efficiently manage thrips in cotton.

Classification

Thrips were first described by De Geer in 1744 under the name of *Physapus*. The widely used term ‘thrips’ was first used by Linnaeus in 1758. Thrips were elevated to their own order by Haliday in 1836. The contemporary order containing thrips is *Thysanoptera*. *Thysanoptera* is defined by possession of a protrusible sac-like arolium at the apex of each leg (Heming 1971), and by their asymmetric mouth-parts in which only the left mandible is developed (Heming 1978). Thrips are further divided into two Sub-orders known as *Terebrantia* and *Tubulifera*. Females of *Terebrantia* each have an external ovipositor of four saw-like valves, while females of *Tubulifera* have an ovipositor which is flexible internally but protrudes externally and appears much like a tube (Mound et al. 1980). This difference between *Tubulifera* and *Terebrantia* is so pronounced that some workers considered organizing *Tubulifera* and *Terebrantia* into two separate orders (Mound et al. 1980). Regardless, there is only one family that is a part of *Tubulifera*. This family, *Phlaeothripidae*, was first made a family by its current name by Uzel in 1895. The family includes 3500 different species, the most of any family of thrips (Mound and Morris 2007). *Phlaeothripidae* is easily distinguishable from the families of *Terebrantia* through simple external observation. *Phlaeothripidae* lacks the characteristic saw-like ovipositor found on females of all *Terebrantia*, excluding

Uzelothripidae. The family of *Uzelothripidae* is part of *Terebrantia*. The organization of *Terebrantia* is more complex than *Tubulifera*.

Most sources claim eight extant families in the *Terebrantians* (Mound and Morris 2007). These eight families of *Terebrantia* are *Uzelothripidae*, *Merothripidae*, *Melanthripidae*, *Aeolothripidae*, *Fauriellidae*, *Adiheterothripidae*, *Heterothripidae*, and *Thripidae* (Mound and Morris 2007). The family that includes *F. fusca* is known as *Thripidae*. *Thripidae* is the second most speciose family in *Thysanoptera* (Mound and Morris 2007). *Thripidae* includes all Thysanoptera with slender trichomes on the third and fourth antennal segments and an abdominal segment ten that is not entirely tubular. Certainly, part of the reason for this concentration of citations is the large proportion of thrips within *Thripidae* that are pests of crops. More than ninety percent of all pest thrips are found in the family *Thripidae*.

Prey and host range

As with other taxonomic groups at the level of order, *Thysanoptera* contains a diverse assemblage of species, each with its own particular host range and prey. More specifically, fungal spore feeders (Mound and Teulon 1995), fungal hyphal feeders (Mound and Teulon 1995), flower feeders (Kirk 1984b), mature leaf feeders (Mound and Teulon 1995), or flower and leaf feeders (Mound and Teulon 1995). The degree of host specificity varies from monophagy to polyphagy regardless of whether the thrips is an obligate predator, fungal spore feeder, fungal hyphal feeder, flower feeder, mature leaf feeder, young leaf feeder, gall former, or flower and leaf feeder.

Because of the large host range of thrips, economic infestations in crops is an inevitability. Those crops include but are not limited to apple, *Malus pumila* (Miller) (Swift and Madsen 1956), asparagus, *Asparagus officinalis* (L.) (Banham 1968), avocado, *Persea americana* (Miller) (Bailey 1938), banana, *Musa paradisiaca* (L.) (El-Bashir and Al-Zabidi 1985), barley, *Hordeum vulgare* (L.) (Bailey 1948), kidney beans, *Phaseolus vulgaris* (L.) (Karel and Mghogho 1985), cabbage, *Brassica oleracea* (L.) (Wolfenbarger and Hibbs 1958), cashew, *Anacardium occidentale* (L.) (Fennah 1963), celery, *Apium graveolens* (L.) (Wisecup and Miller 1933), citrus, *Citrus* spp. (L.) (Hall 1930), coconut, *Cocos nucifera* (L.) (Sakimura 1986), corn, *Zea mays* (L.) (Kucharczyk et al. 2011), cotton *Gossypium* spp. (L.) (Bournier 1994), cucumber, *Cucumis sativus* (L.) (Kawai 1983), flax, *Linum usitatissimum* (L.) (Bonnemaison and Bournier 1964), *Phleum* (L.), forage legumes *Medicago sativa* (L.) (Loan and Holdaway 1955), *Melilotus* spp. (L.) (Loan and Holdaway 1955), *Trifolium* spp. (L.) (Loan and Holdaway 1955), garlic, *Allium sativum* (L.) (Verma et al. 2012), grapes, *Vitis vinifera* (L.) (Yokoyama 1977), leeks, *Allium porrum* (L.) (Theunissen and Legutowska 1991), lettuce, *Lactuca sativa* (L.) (Yudin et al. 1988), millet, *Panicum miliaceum* (L.) (Shpanev and Golubev 2016), olives, *Olea europaea* (L.) (Bournier 1983), onion, *Allium cepa* (L.) (Bailey 1938), pea, *Pisum sativum* (L.) (Williams 1915), peanuts, *Arachis hypogaea* (L.) (Poos 1941), pear, *Pyrus communis* (L.) (Bailey 1938), pineapple, *Ananas comosus* (Miller) (Linford 1932), rapeseed, *Brassica campestris* (L.) (Burgess and Weegar 1988), rice, *Oryza sativa* (L.) (Vidyasagar and Kulshreshtha 1983), safflower, *Carthamus tinctorius* (L.) (Carlson 1964), slash pine, *Pinus elliottii* (Engelmann) (Ebel 1961), sorghum, *Sorghum bicolor*

(L.) (Ananthakrishnan 1971), soybean, *Glycine max* (L.) (Reisig et al. 2012), stonefruit, *Prunus armeniaca* (L.) (Bailey 1938), *P. persica* (L.) (Bailey 1938), strawberry, *Fragaria* spp. (Duchense) (Bailey 1938), sugar beet, *Beet vulgaris* (L.) (Bailey 1938), sugar cane, *Saccharum officinarum* (L.) (Des Vignes 1987), tea, *Carmellia sinensis* (L.) (Dev Vignes 1964), watermelon, *Citrullus lanatus* (Thunberg) (Iwaki et al. 1984), and wheat, *Triticum sativum* (L.) (Bailey 1948). On ornamentals, thrips feed on begonias, *Begonia* spp. (L.) (Eide 1943), calla lily, *Zantedeschia aethiopica* (L.) (Chen et al. 2005), Christmas cactus, *Schlumbergera bridgesii* (Lemaire) (Oetting and Beshear 1980), Chrysanthemum *Chrysantemum* spp. (L.) (Frey 1993a) and *Chrysanthemum Asteraceae* (L.) (Frey 1993a), eucalyptus, *Eucalyptus* spp. (L'Héritier) (Minaei 2012), fig, *Ficus retusa* L. (Avidov and Harpaz 1969), *F. microcarpa* (L.) (Avidov and Harpaz 1969), and *F. benjamina* (L.) (Avidov and Harpaz 1969), gladiolus, *Gladiolus* spp. (L.) (Bournier 1983), *Freesia* spp. (Ecklon) (Eide 1943), *Iris* spp. (L.) (Lewis et al. 1997), gloxinia, *Gloxinia* spp. (L'Héritier), lilly, *Lilium* spp. (L.) (Bailey 1939), orchid, *Orchis* spp. (Tournefort) (Mound 1976), and rose, *Rosa* spp (L.) (Henneberry et al. 1961). The previous list does not cover the major tree crops that thrips infest. Thrips infest more hosts than those listed.

While perhaps not as important as knowing which crops thrips infest, knowing the weeds that thrips infest is also important. Weeds host thrips when crops are not available for thrips to infest (Cho et al. 1995b). Some species of thrips preferentially feed on weed hosts compared with crops (Sites and Chambers 1990). The following list of weed hosts covers some of the hosts of *F. fusca* and *F. occidentalis* in the United States. A survey

conducted in 2002 in North Carolina by (Groves et al. 2002) found *F. fusca* reproducing on German knotweed, *Scleranthus annuus* (L.), common chickweed, *Stellaria media* (L.), dandelion, *Taraxacum officinale* (Wiggers), prickly-sow thistle, *Sonchus asper* (L.), spoonleaf purple everlasting, *Gnaphalium purpureum* (L.), catsear, *Hypochaeris radicata* (L.), wild radish, *Raphanus raphanistrum* (L.), field clover, *Trifolium campestre* (Shreber), ribwort plantain, *Plantago lanceolata* (L.), prickly lettuce, *Lactuca scariola* (L.), Carolina crane's-bill, *Geranium carolinianum* (L.), mouse-ear chickweed, *Cerastium vulgatum* (L.), henbit dead-nettle, *Lamium alexandrinum* (L.), blue toadflax, *Linaria Canadensis* (L.), sheep's sorrel, *Rumex acetoselis* (L.), curly dock, *Rumex crispus* (L.), horseweed, *Erigeron canadensis* (L.), hairy buttercup, *Ranunculus sardous* (Crantz), and American plantain, *Plantago rugelii* (Decaisne). Western flower thrips collected by (Chamberlain et al. 1992) from weeds in 1988 and 1989 showed that *F. occidentalis* can infest narcissus, *Narcissus jonquil* (L.), trumpet creeper, *Campsis radicans* (L.), yellow honey suckle, *Lonicera japonica* (Thunberg), mouseear chickweed, *cerastium vulgatum* (L.), blue cornflower, *Centaurea cyanus* (L.), rabbit tobacco, *Gnaphalium obtusifolium* (L.), dandelion, *Taraxacum officinale* (Wiggers), field bindweed, *Convolvulus arvensis* (L.), wild turnip, *Brassica campestris* (L.), mustard, *Brassica* spp. (L.) iris, *Iris* spp. (L.), henbit, *Lamium alexandrinum* (L.), redbud, *Cercis Canadensis* (L.), black medic, *Medicago lupulina*, crimson clover, *Trifolium incarnatum* (L.), white clover, *Trifolium repens* (L.), arrowleaf clover, *Trifolium vesiculosum* (Savi), smooth vetch, *vicia dasycarpa* (Tenore), day lily, *Hemerocallis fulva* (L.), magnolia, *Magnolia grandiflora* (L.), China-berry, *Melia azedarach* (L.), cutleaf eveningprimrose,

Oenothera laciniata (Hill), common yellow woodsorrel, *oxalis dillenii* (Jacquin), crabapple, *Malus angustifolia* (Aiton), and black nightshade, *Solanum nigrum* (L.). In the same study, (Chamberlain et al. 1992) found *F. fusca* on yellow honey suckle, *Lonicera japonica* (Thunberg), mouseear chickweed, *cerastium vulgatum* (L.), rabbit tobacco, *Gnaphalium obtusifolium* (L.), dandelion, *Taraxacum officinale* (Wiggers), wild turnip, *Brassica campestris* (L.), iris, *Iris* spp. (L.), redbud, *Cercis Canadensis* (L.), black medic, *Medicago lupulina*, crimson clover, *Trifolium incarnatum* (L.), white clover, *Trifolium repens* (L.), arrowleaf clover, *Trifolium vesiculosum* (Savi), day lily, *Hemerocallis fulva* (L.), cutleaf eveningprimrose, *Oenothera laciniata* (Hill), and black nightshade, *Solanum nigrum* (L.). Some hosts, such as rabbit tobacco and *Trifolium* species, can host *F. occidentalis* and *F. fusca*. While feeding on weeds, thrips can become infected with viruses which can be transmitted to plants. Where they transmit viruses from weeds to crops, thrips migrate from weeds to crops in the spring, leading to infestation and infection (Marchoux et al. 1991).

Just as some species of thrips feed primarily on plant leaves or pollen and have occasional predatory feeding habits, some species of thrips are predominantly predatory in their feeding habits and supplement predation with occasional feeding on plant sources. Thrips are known predators of spider mites, *Lepidoptera*, and other *Thysanoptera*. On apple, *Malus pumila*, *Haplothrips kurdjumovi* (Karny) feeds on eggs of codling moth, *Cydia pomonella* (L.), and bud moth, *Spilonota ocellana* (MacPhee 1953). *Leptothrips mali* feeds on *Calepitrimerus baileyi* infesting apple (Bailey 1940b). The European red mite (Koch), *Panonychus ulmi*, is prey to both *Haplothrips kurdjumovi*

(MacPhee 1953) and *Leptothrips mali* (Parrella et al. 1982) when the mite is infesting apple. On citrus (*Citrus* spp.), six-spotted thrips (Pergande), *Scolothrips sexmaculatus*, feed on *Eotetranychus sexmaculatus* (Muma 1955). On cotton, *Gossypium* spp., common blossom thrips, (Trybom) *Frankliniella schultzei*, *Thrips imaginis* (Bagnall), and onion thrips, *Thrips tabaci* (Lindeman), feed on two-spotted spider mite (Koch), *Tetranychus urticae* (Wilson et al. 1996). *Frankliniella occidentalis* and *Neohydatothrips variabilis* (Beach) feed on *Tetranychus* spp. (Dufour) (Gonzalez and Patterson 1982, Lincoln et al. 1953) on cotton. On peach, six-spotted thrips feed on the Pacific spider-mite *Tetranychus pacificus* (McGregor) (Rice and Jones 1972). On sorghum, *Scolothrips sexmaculatus* feeds on *Oligonychus indicus* (Berlese) (Manjunatha and Puttaswamy 1992). On strawberry, six-spotted thrips feed on two-spotted spider mites (Oatman and McMurtry 1966). It is important to remember that thrips are dynamic in their predation habits. For example, *F. occidentalis* can be both a pest and beneficial in cotton in the southeastern United States in the same year. While cotton is in the seedling stage, feeding by *F. occidentalis* is detrimental to the development of the plant (Cook et al. 2011). Once the plant is larger than the seedling growth stage, *F. occidentalis* can be beneficial if it feeds on spider mites (Trichilo and Leigh 1986). Thrips also feed on other thrips species. *Scolothrips sexmaculatus* (Pergande) feeds on *T. pini* (Lewis 1973). *Haplothrips bedfordi* feeds on *Scirtothrips aurantii* (Lewis 1973). *Leptothrips mali* (Fitch) feeds on *F. moultoni* (Bailey 1940a).

In recent years, the distribution of thrips increased in geographic area. For example, *Frankliniella occidentalis* (Pergande), originally only found in western North

America, was reported in Europe, eastern Canada, South America, and Australia in the 1970s (Kirk and Terry 2003). The cause for this larger distribution is not fully known, but globalization (Lewis 1997c) and pesticide use (Kirk and Terry 2003) are most cited. Response to stop the spread of this pest is massive, as one third of all citations concerning *Thysanoptera* involve *F. occidentalis* up to 2009 (Reitz 2009). However, one should not think that *F. occidentalis* is the only thrips that poses a danger to agricultural crops. *F. occidentalis* is a relatively new global thrips pest compared with the other thrips pest species in existence. *Thrips tabaci* (Lindeman), also known as onion thrips, is one of the earliest known examples of an invasive species. They are recorded spreading across the Roman Empire by soldiers carrying onion and garlic (Mound 2005). Onion thrips originally inhabited solely the Mediterranean, but they have been reported damaging crops in North and South America, Europe, Asia, and Australasia (Mound 2005, Boateng et al. 2014). *Thrips palmi* (Karny), also known as melon thrips, have also increased their range as a pest. Originally restricted to its native region of southern Asia before 1980, it now covers most tropical and subtropical locations in the world and greenhouses in temperate areas (Cannon et al. 2007). Another major thrips pest is *Scirtothrips dorsalis* (Hood), also known as the chili thrips. Like, *Thrips palmi*, *Scirtothrips dorsalis*, was originally confined to southern Asia, but since has been identified in Hawaii in 1987 and Florida in 2005. It is not reported in other locations in the United States. All of the previously mentioned species of global thrips pests claim the United States as part of their range.

Distribution of thrips

Thrips as a whole are distributed across all 50 states in the United States (Washburn 1958) (Kirk and Terry 2003). Species that are regionally important in the United States include *Anaphothrips obscurus* (Muller), *Haplothrips aculeatus* (F.), *Caliothrips fasciatus* (Pergande), *Chirothrips manicatus* (Pergande), *Echinothrips americanus* (Morgan), *Frankliniella fusca* (Hinds), *Frankliniella intonsa* (Trybom), *Frankliniella schultzei* (Trybom), *Frankliniella tenuicornis* (Uzek), *Frankliniella tritici* (Fitch), *Heliothrips haemorrhoidalis* (Bouche), *Limothrips cerealium* (Haliday), *Microcephalothrips abdominalis* (Crawford), *Neohydatothrips variabilis* (Beach), *Scirtothrips citri* (Moulton), *Selenothrips rubrocinctus* (Giard), *Sericothrips variabilis* (Beach), *Taeniothrips inconsequens* (Uzel) *Thrips atratus* (Haliday), *Thrips hawaiiensis* (Morgan), *Thrips simplex* (Morison), *Thrips vulgatissimus* (Haliday) (Washburn 1958, Bournier 1994, Kirk and Terry 2003)

Global trade has contributed significantly to the global distribution of thrips. Arguably, the number one thrips pest, *Frankliniella occidentalis*, spread from North America to Europe and eventually to the rest of the world, mostly on ornamental crops grown in the United States which were shipped across the world. (Kirk and Terry 2003). During the 1990's in the United Kingdom, 20.5% of all imported plant cuttings and 12% of all imported plants were infested with *Frankliniella occidentalis* (Frey 1993b). *Frankliniella occidentalis* has since become a global pest on both indoor and outdoor plants (Kirk and Terry 2003).

Biology of thrips

Nearly all *Thysanopterans* in the family *Thripidae* have characteristics of their biology that lend themselves to make thrips such global pests. These include, but are not limited to, the ability to conceal eggs in plant tissue with an ovipositor, a diverse, rapid, and flexible method of reproduction (Lewis 1997c), their sensory ability, dispersal habits, overwintering habits, their minute size coupled with their behavior, their unique lifecycle, their prey and host range, their predators, parasites, and diseases, and their ability to carry and transmit viruses (Yudin *et al.* 1988b).

Life cycle

The life cycle of the typical *Terebrantian* (Thripidae) pest species consists of an egg stage, followed by two active larval instars, two relatively inactive non-feeding pupal instars known as the pro-pupa and the pupa, respectively, and an adult stage. *Tubuliferan* thrips have an additional pupal instar. The average interval for the life cycle takes between 10 and 30 days (Lewis 1997c). However, the amount of time that a life cycle takes varies widely, not only between species, but within a species depending primarily on temperature, and, to a lesser extent, humidity and available nutritional quality (Trichilo and Leigh 1988, Lewis 1997c). For example, egg development for western flower thrips takes nearly twice as long if the temperature is lowered to 15 degrees Celsius from 20 degrees Celsius (Lewis 1997c). This range of developmental time factors into the number of generations possible in one year. In warm regions and greenhouses, 12 to 15 generations can be completed in one year, while some winter climates permit only

one or two generations in one year (Lewis 1997c). What is truly remarkable is how quickly thrips can successfully complete their life cycle.

Reproduction and fecundity

Reproduction in *F. fusca*, *F. occidentalis*, and *F. tritici*, requires copulation between sexually mature members of the opposite sex. Most thrips species lay both fertilized and unfertilized eggs. The mechanism that determines whether an egg becomes fertilized is not known, and, thus, the process of sex determination is not fully understood in thrips (Moritz 1997). Some suggest the information is located within the autosomes (Moritz 1997), although no research or evidence is given. Other evidence cited includes fluctuations in the proportion of males in a thrips population. The frequency of males in some thelytokous populations of thrips depends on the temperature to which the population is exposed. This could indicate that a bacterium is responsible for sex determination in some thrips species. Evidence given includes a similar phenomenon in wasps of the genus *Trichogramma* (Stouthamer and Warren 1993). Although some thrips species do not need sexual reproduction to propagate, this is not the case for the vast majority of thrips species.

Knowledge of fecundity of some pestiferous thrips species are known on key crops, although fecundity varies widely, depending on temperature and nutritional quality of hosts. Specifically, *Frankliniella occidentalis* females were observed laying an average of ninety five eggs in their lifetime at twenty degrees Celsius on Blue Lake Variety green beans (Lublinkhof and Foster 1977). At fifteen degrees Celsius, the average offspring per female was twenty four on the same Blue Lake Variety green beans. The eggs took an

average of six days to hatch when the thrips were reared at twenty degrees celsius (Lublinkhof and Foster 1977). Other researchers show that *F. occidentalis* adults averaged sixty offspring for each female when reared on Acala SJ-2, but only an average of five offspring per female on Pima S-5 (Trichilo and Leigh 1988). The fecundity of *F. occidentalis* is significantly connected to nutrient availability, specifically protein from spider mite eggs and pollen. In the same study in which females averaged sixty offspring on Acala SJ-2 leaves alone, females fed spider mite eggs averaged eighty offspring, and females fed pollen averaged one hundred and ninety five offspring (Lublinkhof and Foster 1977). The overall rate of fecundity of thrips is highly variable given the specific temperature, humidity, and nutritional quality of hosts.

Types of reproduction, sex ratios, and genetics vary among *Terebrantia*. Yet, all families of *Terebrantia*, excluding *Uzelothripidae*, bear the unique saw-like ovipositor that allows them to oviposit directly into plant tissue. The *Terebrantian* female will vertically insert the ovipositor into the desired tissue. The female will then push its abdomen backwards which will cause the ovipositor to pivot on its basal articulation. When the ovipositor pivots, it will mechanically extend from its sheath and become perpendicular to the abdomen and the plant tissue. The thrips will then work the ovipositor into the tissue and use the saw-like blades of the ovipositor to cut the tissue. The saw-like blades will separate to allow the egg to be deposited into the tissue (Moritz 1997). Some species seal off the incision with a drop of fluid secreted from the depositing female, while others embed the egg deep enough to be completely covered with tissue. The time required to oviposit completely usually takes a few minutes and

females either feed or rest after laying each egg (Moritz 1997). Eggs tend to be laid in older non-expanding tissue to avoid crushing. Several thrips species are known to lay on artificial surfaces such as stretched parafilm membranes. These include *F. occidentalis*, a close relative of *F. fusca*. Thrips that perform this behavior are usually generalists (Moritz 1997). *F. fusca* is named among those thrips that oviposit their eggs directly into plant tissue, as are *T. tabaci*, *F. occidentalis*, *F. tritici*, and *N. variabilis*, the most numerous thrips found infesting seedling cotton in the United States (Cook et al. 2003, Reed et al 2010, Reay-Jones et al. 2017, Wang et al 2018).

Egg stage

Eggs of thrips vary widely depending on the species of thrips that produces the egg. Most eggs that are laid in the tissue of plants by *Terebrantia* are smooth to accommodate easier oviposition and are kidney shaped. *Tubulifera*, which lays its eggs on the surface of the desired material, can have eggs that are pentagonal or hexagonal shaped and fixed to the host with a sticky patch. The color of thrips eggs are white, yellow, or darkly colored. Eggs that are clear and laid in plant tissue can be difficult to detect, even with a microscope. The eggs of *Terebrantians* have an anterior operculum which is removed by a saw-shaped oviruptor at hatching (Moritz 1997). Even more amazing than the diversity of the shape and color of thrips eggs is the biological process that occurs inside the eggs and is responsible for the majority of the organ systems that are found inside thrips. The following description of the thrips life cycle seeks to find commonalities found between most thrips species, especially those that are pestiferous.

As soon as an egg is deposited into plant tissue, the embryo begins to separate from the yolk (Moritz 1997). The structure of the embryo is still attached to the inside of the egg wall at this point and will start to lengthen. Once the embryo is at the appropriate length, the embryo will separate from the inside of the cell wall where segmentation of the embryo will occur (Moritz 1997). The antennae and legs will form first followed by the gnathal appendages. Following gastrulation and the closing of a few extra-embryonic germ cells, the embryos orientation within the egg will change completely. The serosal cells at the anterior end of the egg contract and form the secondary dorsal organ. The amnion rolls back and replaces the serosa as a primary dorsal closure. Katatrepsis takes one to two hours in *Frankliniella occidentalis*, *Hercinothrips femoralis* (Reuter). These three species are the topic of description of the larval instars, pupal stages, and adult stage descriptions that follow. Once katatrepsis occurs, the sensory system, circulatory system, muscle system, digestive tract, and nervous system of the thrips are functional (Moritz 1997). Once these organs are functional, the thrips has completed its development in the egg stage and will soon hatch into an immature thrips.

Immature thrips resemble a miniature version of the adult, only the immature lacks wings and genital appendages. Immature thrips are often yellow or pale in color, though not in every case. The color is contained in their cuticle (Moritz 1997). Both first and second instars grow in width and length, which makes discerning the first instar from the second instar difficult, especially between late first and early second instars. Both first and second instar larvae have similar mouthparts to adults in that they function as a ‘punch and suck’ type action (Moritz 1997). The mouthparts are comprised of two

laciniae with the left mandible enclosed within a hypognathous mouth cone, but lack gnathal stylets found in adults. Although the mouthparts are not fully developed in immature instars, they can still feed on *Tetranychus* eggs (Wilson et al. 1996) and pollen (Zhi et al. 2005), assuming the structures are small enough for the immature thrips to feed on them. The antennae are similar to adults and they have the campaniform sensillum already developed (Moritz 1997). The compound eyes are not yet developed; the immature uses four stemmata to see (Moritz 1997). Ocelli are absent in all larval forms. The wings and genital appendages are not developed in the immature, but the fore and hind wing discs will begin forming late in the second instar larval stage (Moritz 1997). Other structures found in the adult will not begin development until the pupal stage begins.

The pupal instars are distinguished from the immature instars by the presence of a colorless cuticle covering the body of the pupa. The developing compound eyes, ocelli, and gnathal stylets are visible through the cuticle (Moritz 1997). The organism in the pupal stage will be inactive and will not flee if touched. If the thrips adult is winged, the first and second pupal instars are distinguished by the length of wings. If the length of the wings of the pupa are at full length then the pupa is in the second pupal stage. If the wings are shorter than full length, the organism is still in the first pupal stage. The musculature of the wings in the pterothorax begins immediately once the propupal molt is finished (Moritz 1997). The changes to the digestive system are significant during the pupal stage. The midgut shortens and the epithelium disappears (Moritz 1997). Another change as significant as the change to the midgut, is the development of the reproductive

organs. This development does not occur until the thrips leaves the immature stage. The ovary in female thrips will begin to divide from the anterior end into the four ovarioles. On the exterior of the organism, the meso and metathorax fuse more firmly to the pterothorax (Moritz 1997). While most structures that are present in the thrips adult are developed when the thrips emerges from the pupae, there is evidence that suggests that some minor structural development occurs only once the thrips is an adult.

Evidence suggesting, but not proving that further development occurs at the adult stage is the fact that thrips must usually wait before mating can begin (Terry and Schneider 1993). *Frankliniella occidentalis* must wait 24 hours before mating will occur (Terry and Schneider 1993). Nearly all *Thysanoptera* can mate within 2 to 3 days of eclosion from the pupae (Terry 1997). Structures needed for flight also require further development as an adult before flight can occur (Lewis 1997b). Length of time for general development after emergence from the pupae at 20 degrees Celsius is cited at 5 hours in *Limothrips cerealium* (Lewis 1973). Authors believe that shorter times are common in tropical species of thrips (Lewis 1997b). Besides development of wings and development of reproductive organs, all other structural systems are fully functional once the thrips ecloses from the pupae. Some of these structures have not changed significantly from the immature instar, while others have changed drastically. For, example the antennae of thrips do not change much from the larval stage to the adult stage. They are comprised of four to nine, but most commonly, seven to eight segments (Moritz 1997). Other structures change completely. Compound eyes are added in the pupal stage and are located between the vertex, clypeofrons, and genae (Moritz 1997). The number of cells in

the eye can range anywhere from two to three, to so numerous that they nearly completely cover the head of the thrips (Mound and Heming 1991). The lenses can be colored on the ventral surface to distinguish species in some cases (Moritz 1995). If the species has wings, they will also have three ocelli situated dorsally on the head capsule, usually in the shape of a triangle (Moritz 1997). The length, position, and number of setae on the head and in relation to the ocellar triangle are important taxonomic characters for identification of adults (Moritz 1997). While some structures take time upon eclosion from a pupa to become fully functional, the same phenomenon can occur if an adult thrips overwinters. Adults that overwinter in some species need a second period of teneral development to reactivate their flight muscles (Lewis 1963). This only occurs in species that overwinter and does not occur in all species of thrips.

Overwintering

Some thrips species live in environments where breeding and feeding activity is not completely halted by low temperature in winter. Thrips in climates with cold winters can overwinter as larvae or pupae in the soil (Brose et al. 1993), as adults on crops or weeds (North and Shleton 1986), in leaf litter (Lewis and Navas 1962), or in tree bark (Tree and Walter 2012). Understanding the pupation and dormancy of thrips that overwinter, the mortality overwintering populations might face, and the emergence of the thrips population can give insight into thrips flights into crops after dormancy (Morsello et al. 2008). These insights into thrips flights are generalized into parameters that are easier to measure than the number of thrips that pupate, overwinter successfully, and emerge successfully.

Many *Terebrantians* overwinter as pupae in the soil. Pestiferous species of thrips, such as *F. fusca* and *F. occidentalis* are known to overwinter on weeds and winter crops. (Chamberlain et al. 1992). These species are known to pupate both on plants and on the soil surface (Kirk 1997) (Ansari et al. 2008). Thrips that pupate or overwinter at the surface of the soil or on a plant can breed during odd warm times during winter months and are the first to find host plants in the spring (Kirk 1997). Pupae and adults are the only forms of thrips that are regularly found overwintering. Larvae of *Aeolothrips albicinctus* (Haliday) (Wetzel 1963) and eggs of *Scirtothrips citri* (Rhodes et al. 1989) are found in winter months or in winter months of warm climates, but are not considered the true overwintering form, as their pupal or adult overwintering form is more tolerant to cold. The vast majority of thrips overwinter as adults or pupae.

Thrips exposed to overwintering environments enter a state of dormancy. This dormancy can range from a complicated environmentally induced diapause, seen in *Anaphothrips obscurus* (Muller) (Kamm 1972), to a temperature induced quiescence that is quickly reversed, once temperatures are increased (Sites and Chambers 1990). If a thrips delays molting, egg laying, or reproduction, it is considered in a state of dormancy. Feeding does not indicate that a thrips is no longer dormant (Kirk 1997). Variation in factors that induce winter dormancy in thrips can occur even between species. Certain glasshouse strains of *Frankliniella occidentalis* do not enter diapause, even when exposed to short photoperiods (Danks 1971), which is a main driver of diapause in thrips (Kamm 1972).

When thrips overwinter, whether through diapause or dormancy, mortality can be extremely high. Under normal field conditions, mortality of 80 percent is observed in *Thrips calcaratus* (Uzel) in Wisconsin (Raffa et al. 1992). Mortality occurs from freezing (Kirk 1997), drowning (Bailey 1933), or desiccating (Kirk 1997) in both soil dwelling and above ground dwelling thrips. Rainfall drowns adults exposed to it when they overwinter and will drown larvae that are on the ground preparing to pupate in the soil. Thrips species that pupate in soil during the summer also have high rates of mortality, especially under dry soil conditions (Andrewartha 1954). Thrips that survive overwintering rely on several cues to determine when they will become active again.

If a species of thrips overwinters in the soil, soil temperature is the best indicator for determining when it will emerge from the soil (Bailey 1944). This is the only external cue that soil dwelling thrips can detect while they overwinter in the soil (Kirk 1997). Early plowing will trigger an earlier emergence, if thrips are exposed to higher temperatures at the soil surface, and a heavy cover crop will delay emergence (Bailey 1934). Once emergence begins, the rate of emergence is variable in relation to temperature until the population of thrips have all emerged. During periods that are warm and dry, the rate of emergence is greater than in periods that are cool and wet (Foster and Jones 1915, Buhl 1937, Bailey 1944). Thrips that overwinter above ground do not rely on the soil temperature as a cue to emerge from overwintering sites. These thrips use air temperature. Rather than begin emergence as soon as a temperature threshold is exceeded, these species emerge after a certain amount of degree days. For example, *T. tabaci* begin reactivation after 88 degree days have accumulated using a base of 6.67

degrees Celsius (Sites and Chambers 1990). These estimates have limitations, as variations in temperature nearly always occur in natural settings, and some activity before and after the degree day threshold is met is likely to occur (Lewis 1963).

Simply modeling the emergence of a population of thrips is not enough to understand how large a population can become given a certain amount of time. Knowing how quickly a population can increase, rates of predation and parasitism, combined with rainfall and temperatures, are needed to have the best idea of how large a thrips population can become (Tamò et al. 1993). Once a model describing the population dynamics of a thrips pest is functional, thrips densities recorded on traps can be related to damage ratings found on plants. In this way, data such as rainfall and temperature can be used to determine the potential for damage on crops susceptible to thrips (Kirk 1997).

Communication and host cues

Members of all thrips species, whether or not they require sexual reproduction to survive as a species, need a way to communicate. Use of sex pheromones for attracting members of the opposite sex over long distances is not documented for thrips. Instead, thrips are attracted to a host plant or flower where they will find mates (Terry 1997). Host selection involves a series of long range and short range cues. In research, these cues are inferred through examining landing rates, number of adults, number of larvae, and thrips damage (Terry 1997, Faircloth et al. 2000, Hoddle et al. 2002). The factors that determine whether a thrips recognizes a plant as a host depend on whether or not a thrips has landed on a host, and there are numerous factors that determine initial host selection.

Thrips are known to locate hosts using color (Kirk 1984a), size (Stoddard 1986), and volatiles associated with the host (Knudsen et al. 1993), before they make physical contact with the plant. Because mating and oviposition often occur on the same host as feeding, the same cues are likely used to find a host for reproduction (Terry 1997). Color and contrast are by far the predominant cues used by most thrips species. Color alone is enough to attract some thrips species (Kirk 1984a), although color and volatiles together are more attractive to thrips. Some of the important aspects of color are wavelength of the light emitted by the surface (the color) (Kirk 1984a), the saturation of the hue (Matteson and Terry 1992), and the brightness of the color (Matteson and Terry 1992). Of the thrips species tested, males and females exhibited similar responses to color (Kirk 1984a). Grass feeding thrips are the least sensitive to changes in color of a host, while anthophilous thrips are the most sensitive. Polyphagous thrips are somewhere between the two in their sensitivity to color changes. Although, the previous generalization is not always the case. *Frankliniella fusca*, a polyphagous species, is less sensitive to changes in color than some grass feeding thrips such as *Limothrips denticornis* (Haliday) (Kirk 1984a) (Cho et al. 1995b). Some of the thrips that are more sensitive to color changes, such as *F. occidentalis*, are also sensitive to ultra violet (UV) ray reflections. Crops with mulches that absorbed UV light were infested with fewer thrips than crops with mulches that reflected UV light) (Kawai 1986). In addition to floral color, differences in flower morphology and size are a factor in some cases. A certain cultivar of *Chrysanthemum* known as the spider type, has a ray florets on which are more difficult for thrips to feed extensively. Fewer thrips were found on spider type chrysanthemums than other cultivars

(De Jager et al. 1995). Size of plants also plays a part in thrips infestations. Tall, lush, green plants attract more thrips than plants that are shorter and less green (Stoddard 1986). A plant's stage of phenology also has an effect on whether a thrips will see it as a potential host (Reay-Jones et al. 2017). Plants that are flowering will generally contain more thrips than those plants that are not flowering (Yudin et al. 1988), but thrips are attracted to both floral and non-floral odors. Thrips will use floral odors alone to locate a host in some cases, but more thrips accept an object as a host if odors and color are used together (Frey et al. 1994). The previous examples describe the cues that encourage a thrips to land on a potential host. The cues to encourage a thrips to feed on the host once it has landed are slightly different.

Short range cues

Evidence for the separation of cues to land is cited by *T. palmi* and its interaction with tomato plants. *T. palmi* will not feed on certain tomato plants, though it will land and explore the leaves of most tomato plants (Hirano et al. 1994). *T. palmi* will also lay fewer eggs on certain tomato plants compared with more favorable hosts suggesting that some chemical cues for oviposition exist at a short range (Kawai 1986). Cotton plants with high proportions of secondary metabolites, such as gossypol, are less damaged from thrips due to less thrips feeding (Gopichandran et al. 1992). Other than chemical cues, some physical cues exist that can shed light on how thrips decide to feed on and colonize a host when they make physical contact with a host.

Thrips must be able to insert their maxillary stylets deep enough into plant tissue to extract liquids. Some researchers found that plants with thick lower epidermis cells

generally hosted less thrips compared with plants with thinner lower epidermis cells. (Gawaad et al. 1973). The cultivars found with less thrips had epidermal cells 10-13 nanometers wide, while the cultivars with more thrips contained epidermal cells about 6.5 nanometers wide. Other researchers found that the maxillary mouthparts of most thrips species extend well beyond the width of the epidermal cells of both the susceptible and resistant varieties (Wiesenborn and Morse 1988). This suggests that thrips receive some feedback on thickness as they probe a potential host with their mouthparts. In a similar manner to thick epidermis cells, cotton leaves with more pilosity were shown to receive less damage and infestation from thrips (Gopichandran et al. 1992). Researchers suggest that restricted movement of thrips and reduced rates of host acceptance for pilose cotton post-alighting are the driving factors behind reduced susceptibility of cotton with high pilosity.

While pheromones between thrips do not play a large part in thrips biology at a long range, at a short range, thrips excrete alarm pheromones, sex pheromones, defensive allomones, and can detect a multitude of olfactory and gustatory stimuli, giving them vital information about their surroundings. Rather than utilize a pheromone at long range to facilitate reproduction, in some species of thrips, males produce an aggregation pheromone that attracts members of both sexes (Hamilton 2005). Anthophilous thrips in particular exhibit these aggregations on flowers, where the main activity is mating, and feeding and oviposition are reduced (Morison 1949, Kirk 1985, Terry and Dyreson 1996). These aggregations also occur on white surfaces similar to flowers (Matteson and Terry 1992). This suggests that long range host cues from potential hosts and not from

other thrips are the driver for these aggregations, at least until the thrips land. Most diversity in alarm pheromones and defensive allomones comes from *Tubulifera*. Most thrips, including *Terebrantia*, excrete these pheromones through an anal cavity (Buffa 1911, Hodson 1935, Lewis 1973). The defensive chemical of only one *Terebrantian*, *Frankliniella occidentalis*, has been identified. These extracts, known as dodecyl acetate and decyl acetate, when used alone or in combination, trigger an alarm response in *Frankliniella occidentalis* (Teerling et al. 1993a, Teerling et al. 1993b). This response induces adults to fly away, second instars to drop off of the plants, and reduced oviposition (Teerling et al. 1993b). The range for the chemical is short enough that thrips will still land on plants near the alarm pheromone. The two chemicals also act as attractants for predators of *F. occidentalis*, such as predatory ants, *Orius*, and *Amblyseius cucumeris* (Teerling 1995). This type of pheromone is not known in any other *Terebrantian* species.

Dispersal habits and population dynamics

While pheromones play only a small part in the dispersal habits of most economically important thrips species, environmental factors are key to understanding thrips dispersal. In some cases, 78% of thrips population movement is explained by environmental factors alone (Davidson and Andrewartha 1948). Environmental factors cause thrips populations to fluctuate dramatically, and populations can seemingly appear or disappear within one year, one month, one week, or even one day (Buhl 1937), depending on the circumstances. These changes in population are almost always a result

of an environmental factor. While most of these factors are abiotic and include heat, drought, cold, and rain, others are biotic and include predators, diseases, and competition.

Of the abiotic factors that contribute significantly to the dispersal habits and population dynamics of a thrips population. Heat is known to cause differences in thrips fecundity (Lowry et al. 1992). The development rate of *Frankliniella occidentalis* becomes slower when the ambient temperature is raised above 30 degrees Celsius (Gaum et al. 1994). Predictably, thrips are able to handle higher amounts of heat when they are exposed to a favorable level of humidity or are given adequate access to water. *Thrips tabaci*, successfully reared at 27 degrees Celsius in dry conditions, were also reared at 38 degrees Celsius, if the air was kept adequately moist (MacGill 1937). The effect of heat on thrips is dependent on other environmental factors. Heat is also known to cause changes in the dispersal of thrips between plants and have an impact on migratory patterns. Some researchers suggest that thrips prefer to disperse during the hottest part of a day (Lewis 1997 b). Recent researchers suggest that this is not always the case. Western flower thrips were found to prefer flight at 28 degrees Celsius compared with 32 degrees Celsius and 24 degrees Celsius (Liang et al. 2010). Further contradicting the claim of peak thrips flight at mid-day is another study by other researchers who observed that 85% of all thrips caught on sticky traps were caught in the morning and in the evening (Ben-Yakir and Chen 2008). Kirk (1997) observed that during periods of intense heat, thrips are found hiding in protected sites within plants, such as in the crevices of leaves or below vegetation. Thrips activity is not regulated by time of day, but by factors

that are sometimes associated with a particular time of day such as heat, humidity, and light. Indeed, heat affects thrips dispersal in relation to other factors.

In natural environments, low moisture of the environment or drought is most likely to affect thrips populations through the desiccation of larvae and pupae. For example, in southern Australia, populations of *Thrips imaginis* reduce significantly during the summer as dry soil makes completion of the pupae stage difficult (Andrewartha 1954). The effect of drought on pupation, which indirectly effects the ability of a population to successfully reproduce to adulthood is dependent, in part, on the soil type of the environment and thrips pupation depth. It is no wonder then that effects of dryness are shown to be beneficial (Bailey 1933) and detrimental to thrips populations (Andrewartha 1954). In general, researchers agree that thrips populations perform best at 70-90% relative humidity (RH) (Kirk 1997). Just as temperature effects the number of thrips that fly within a population (Liang et al. 2010), relative humidity (RH) also plays a part. Western flower thrips were most likely to fly to a new host at 70% RH (Liang et al. 2010). In the same study, more thrips took flight at 50 and 60% RH than at 90% RH. While abiotic factors play a major part in thrips dispersal directly, the affect that biotic factors have on thrips populations should not be discounted.

Populations of *Thrips imaginis* are known to nearly disappear following the shedding of flowers in the summer in southern Australia (Andrewartha 1954). Thrips are significantly affected by the phenological growth stage of available food sources and the type of biological resources available. *F. occidentalis* is known to inhabit *Secale cereale* (L.) and *Medicago sativa* (L.) in North Carolina as early as February (Chamberlain et al.

1992), in which populations of adult females are cited at 124 individuals per 25 flowers (Chamberlain et al. 1992). When either of the crops begin senescence, thrips disperse and infest nearby crops and other hosts. In addition to inhabiting plants based on overall plant age, thrips preferentially inhabit specific parts of a plant. For example, *F. tritici* is known to infest cotton flowers, but is found in far fewer numbers on terminals and bolls (Reay-Jones et al. 2017). Just as plant age and phenology affect the growth and spatial distribution of a thrips population, the size of the population coupled with competitors for resources affect the population dynamics and dispersal.

Thrips as agricultural pests

As previously mentioned, thrips infest a wide variety of agricultural crops, including field crops, field and glasshouse vegetables, ornamentals, and tree crops. In addition to the wide variety of crops thrips can infest, thrips infest a wide geographic area, including all continents other than Antarctica (Kirk and Terry 2003). Thrips feeding can damage plant leaves (Watts 1937) and fruit (Salguero Navas et al. 1991). The damage they cause to crops is comparable to that caused by whiteflies (Aleyrodidae), aphids (Aphididae), scale insects (Coccoidea), and mealy bugs (Coccoidae) (Lewis 1997c). Examples of potential percentage yield losses on crops are 33% on alfalfa, *Medicago sativa* (L.) (Wolfenbarger and Hibbs 1958), 50% on carrot, *Daucus carota* (L.) (Bailey 1938), 40% on cotton, *Gossypium hirsutum* (L.) (Watts 1937), 30-90% on cowpea, *Vigna unguiculata* (L.) (Bal 1991), 34-43% on onion, *Allium cepa* (L.) (Fournier et al. 1995), and 100% on tea, *Camellia sinensis* (L.) (Benjamin 1968). Thrips are an important pest of upland cotton in the United States.

Gossypium hirsutum (L.), more commonly known as upland cotton, is grown on around 30 million hectares of cotton each year globally. In large part, the 2015 national average of \$3.70 per hectare cost of in-furrow and at-plant insecticides is spent for controlling *Frankliniella fusca* (Hinds) (Williams 2016). For a farmer to successfully transition from summer grain production to cotton production, they need to know how to prevent and treat their cotton for thrips, which were the number one insect pest group of cotton in the United States in 2015 (Williams 2016).

Although there are a number of species of thrips found on cotton, about twelve species can reproduce and cause damage to the crop. Of these twelve species, five species regularly infest cotton in the Cotton Belt in the United States. Of these, *F. tritici*, *F. fusca*, *F. occidentalis*, *T. tabaci*, and *N. variabilis* are considered pests of seedling cotton in the United States (Bournier 1994, Cook et al., 2003, Cook et al., 1999, Reay-Jones et al., 2017, Wang et al. 2018), with *F. fusca* being the most important species. Specifically, *F. fusca* is a pest of cotton seedlings in Alabama (Cook et al., 2003), Arkansas (Reed et al. 2010) Georgia (Lambert 1985), Louisiana (Eddy and Sharp, Reed et al. 2010), Mississippi (Dunham and Clark 1937, Reed and Jackson 2002), Missouri (Reed et al. 2010), North Carolina (Reed et al. 2010), South Carolina (DuRant et al. 1994, Reed et al. 2010), Tennessee (Cook et al. 2003), Texas, and Virginia (Reed et al. 2010). Western flower thrips, or *F. occidentalis* is a pest of cotton seedlings in Alabama (Cook et al. 2003), Arkansas (Reed et al. 2010), California (Bailey 1938), Georgia (Cook et al. 2003, Reed et al., 2010), Louisiana (Reed et al. 2010), Mississippi (Reed 1988, Reed et al. 2010), Missouri (Reed et al., 2010), North Carolina, (Reed et al., 2010), Oklahoma

(Karner et al., 1992), South Carolina (DuRant et al., 1994), Tennessee (Cook et al., 2003), Texas (Reed et al., 2010), and Virginia (Reed et al. 2010). Onion thrips, or *T. tabaci*, is a pest of seedling cotton in Arkansas (Reed et al. 2010), Louisiana (Eddy and Sharp 1938), South Carolina (Watts 1937a) (Reed et al. 2010), Tennessee (Cook et al. 2003) (Reed et al., 2010) Texas (Reed et al. 2010), and Virginia (Reed et al. 2010). Eastern flower thrips, or *F. tritici*, are a pest of cotton seedlings in Alabama (Cook et al. 2003), Arkansas (Reed et al. 2010), Georgia (Lambert 1985, Wells et al., 2002), Louisiana (Eddy and Sharp 1938) (Reed et al. 2010), Mississippi (Dunham and Clark, 1937) (Reed and Jackson 2002), Missouri (Reed et al. 2010), North Carolina (Reed et al. 2010), South Carolina (Watts 1937a) (Reed et al. 2010), Tennessee (Cook et al. 2003), and Virginia (Reed et al. 2010). The species *N. variabilis* is known to infest seedling cotton in Alabama (Cook et al. 2003), Arkansas (Reed et al. 2010), Georgia (Reed et al. 2010), Louisiana (Burriss et al. 1980, Reed et al. 2010), Mississippi (Dunham and Clark 1937) (Reed and Jackson 2002), Missouri (Reed et al. 2010), North Carolina (Reed et al. 2010), South Carolina (Watts 1937a) (Reed et al. 2010), Tennessee (Cook et al. 2003), and Virginia (Reed et al. 2010).

Cotton hosts *F. fusca* at all growth stages of development (Reay-Jones et al. 2017). Although cotton hosts tobacco thrips and a complex of other thrips species at all phenological stages, economic damage generally only occurs during the seedling stage of development, defined here as all growth between emergences of seed leaves (cotyledons) and unfurling of the 5th true leaf. Conveniently, infestations of *F. fusca* are most populous during the seedling stage of development and are the dominant species of thrips found

during the seedling stage of development in the southeastern United States (Reay-Jones et al. 2017). Tobacco thrips also inhabit terminals, squares, flowers, bolls, lower leaves, middle leaves, and upper leaves in cotton plants (Reay-Jones et al. 2017). Tobacco thrips, and other species of thrips are most damaging to cotton when they infest the seedling stage of growth.

When adult and immature thrips feed on cotton foliage, they ingest the contents of the epidermal cells of the plant (Cook et al. 2011). The possibilities of damage that infestations of *F. fusca* or other thrips cause to a cotton plant is variable. Under light injury, the cotton leaves will curl at the tips of the leaves, at this level of damage yield loss is negligible. Moderate injury is associated with economic injury and is often the level at which an insecticidal treatment is applied. At severe damage, loss of apical dominance from loss of terminal, or death of the cotton plant occurs. Authors note that cotton is both capable and incapable of recovering yield from early season thrips damage (Sadras and Wilson 1998). In cases of severe thrips infestation or typical thrips infestations supplemented with periods of cool weather between 15 and 20 degrees Celsius, damage from thrips is more likely to cause delayed growth and yield loss. Although yield losses of 11% are possible, recent estimates of losses to thrips range from 0.12% to 0.88% across the Cotton Belt (Cook et al. 2011).

In 2015, thrips were the number one pest of cotton in the southeastern United States (Williams 2016). Thrips infested over 6.6 million acres of cotton. Losses to thrips were estimated at (0.831%) for 2015. The total cost of thrips management nationwide exceeded \$60 million dollars. For comparison in the same year, the losses from *Lygus*

spp. (Hahn) plant bugs were estimated at 0.787%, bollworm/tobacco budworm were 0.462%, stink bugs were 0.436%, and cotton fleahoppers were 0.353% (Williams 2016). Between 2011 and 2016, thrips were consistently placed in the top three pests of cotton on a national level (Williams 2012-2017).

Control strategies

Because thrips are perennial pests of cotton, numerous strategies of integrated pest management (IPM) have been used to control them in the crop. These control measures include, but are not limited to, chemical control, biological control, physical control, reproductive control, regulatory control, environmental control, and cultural control. No one category should be repeatedly used alone, as a more integrated approach will provide the best long-term solution to managing thrips in cotton.

The application of chemical controls is substantially more sophisticated today than it was fifty years ago, but some of the most effective insecticides are among the oldest materials still used in the crop. The establishment of economic thresholds, use of several classes of insecticide (Lewis 1997), alternative chemical delivery methods (Hanna 1958), its speed of delivery and quickness, its reliability and effectiveness make chemical control an attractive choice for thrips management. Chemical control is not without drawbacks and should not be the only option implemented against thrips. Resistance to insecticides by thrips (Huseth et al. 2016) and uncertainty of future insecticide availability make chemical control as a sole treatment ill-advised.

The first chemical control programs for thrips, including *F. fusca*, was not specifically applied for thrips and made use of DDT, disulfoton, phorate, and dicrotophos

(Watson 1965). The number of thrips in the field were not monitored prior to treatment. Treatment for thrips were based on the presence of the boll weevil, *Anthonomus grandis* (Boheman), in the field or on an automatic spray schedule (Watson 1965). More sprays than necessary were applied to cotton. Spraying insecticides without an economic threshold resulted in more expenses for control of thrips than necessary. Currently economic thresholds are available in all southeastern states (Cook et al. 2011). All thresholds include the presence of injury before treatment is justified (Cook et al. 2011). Besides presence of injury, thresholds vary between states. Before calculating an economic threshold, one needs to know the economic injury level. This is the level of thrips infestation that results in economic loss to the crop. Equations are available that calculate economic injury levels (Pedigo et al. 1986). Critical to the establishment of an economic threshold is the damage equation for thrips density. This equation predicts the maximum density that a thrips population will attain and the possibility of economic damage (Fournier et al. 1995). Establishment of thresholds is particularly difficult because environmental conditions change from year to year, as do the dynamics of an insect population (Fournier et al. 1995). For this reason data for economic thresholds are collected from multiple locations over a period of at least two years (Fournier et al. 1995). By supplementing visual counts of thrips with visible economic damage, economic thresholds reduce the uncertainty of thrips population damage and make useful economic treatment of thrips clearer to producers. Once an economic threshold has been established, producers can make full use of the different classes of insecticides available in an efficient and economically acceptable manner.

Classes of insecticides identified by the Insecticide Resistance Action Committee (IRAC) (Sparks and Nauen 2015) that have potential use on thrips include: 1A, carbamates (Jones et al. 2015); 1B, organophosphates (Palumbo 2005); 4A, neonicotinoids (Jones et al. 2015); 5, and spinosyns (Palumbo 2005). Some classes of insecticides, such as organochlorines in the form of endosulfan, are used for thrips in other countries (Lewis 1997). Each class of insecticide is also categorized into different modes of action (Sparks and Nauen 2015). A mode of action describes how the substance in question kills or renders the insect unable to cause problems. (IRAC 2017) While most mode of actions available for control of thrips could theoretically affect thrips, only group 1A, the carbamates, 1B the organophosphates, and group 3A, the neonicotinoids are practical in their application against thrips in cotton. Of these modes of actions, only acephate and phorate (organophosphate), aldicarb (carbamate), thiamethoxam (neonicotinoid), and imidacloprid (neonicotinoid) are available in cotton.

Within each class of insecticide are individual compounds; each with varying effectiveness against thrips. While one chemistry might be more efficacious than another in a lab setting, constraints with the field application can drastically change the efficacy of an insecticide. Method of delivery (McAllister et al. 2003), temperature (Jones et al. 2015), weather (Jones et al. 2015), wind (Murphy et al. 2000), timing of spray (Lewis 1997), and size of host plants (Lewis 1997) alter the ultimate efficacy of an insecticide against thrips under field conditions. The most widespread foliar treatment of thrips in cotton is acephate, an organophosphate. The timing of foliar treatments is critical. Spraying too soon leaves new growth potentially susceptible and increases the probability

of a follow up treatment. Spraying too late wastes resources and does not stop damage. Most recommendations suggest spraying before the second true leaf stage (Jones et al. 2015). While the delivery of most chemicals to control insects are foliar sprays, control of thrips in cotton relies mostly on relatively new forms of delivery (Cook et al. 2011). These delivery methods are seed treated with an insecticide and in-furrow sprays. The insecticide is taken up by the plant and systemically spread throughout its structures. Aldicarb, phorate, acephate, and imidacloprid are available as in-furrow granular or in-furrow sprays. Thiamethoxam and imidacloprid are available as seed treatments. In South Carolina, cotton planted after May 20 sees benefits from seed treatments and cotton planted before May 20 sees benefits, albeit at a reduced efficacy the farther from May 20 the date is (Jones et al. 2015). Cold weather, drought, or excess rain all reduce the efficacy of seed treatments and in-furrow treatments (Jones et al. 2015). Systemic treatments are further weakened by the size of the plant. A single dose of systemic pesticide is usually applied to plants. The concentration of the pesticide becomes diluted as the plant grows, until it no longer has any effect. While the application method of an insecticide and the prevailing environmental conditions at application have a major effect on determining whether an application will successfully manage thrips, the biology of the specific thrips population also plays a role in determining whether an insecticide program will be successful.

Although pesticide resistance occurs in host-specific species, the biology of opportunistic species can lead to rapid resistance evolution because of rapid generation turnover and rapid colonization time (Winemillar 1992, Parker et al. 1995). Other factors

suggested as the culprit for rapid resistance development are polyvoltinism and high reproductive potential. Producing more than one generation in a crop season means that selection can occur on multiple generations. Inbreeding occurs abundantly in thrips, which are haplodiploid (Lewis 1973). Females that are unfertilized produce sexually viable males, containing only the mother's genes, which then mate viably with the mother to produce more female offspring. This way, resistant genes are not bred out of a population as easily. In *F. fusca*, all of the biological attributes that heighten the risk of pesticide resistance are present. Recently, populations of *F. fusca* were reported as tolerant to neonicotinoid pesticides (Huseth et al. 2016). This distribution of reduced susceptibility of thrips to neonicotinoids is found in parts of Louisiana, Arkansas, Mississippi, and Tennessee along the Mississippi River. East Texas also includes resistant populations, though more sparse in number and level of resistance (Huseth et al. 2016). No specific genes are implicated for resistance to neonicotinoids in tobacco thrips. Prophylactic use of neonicotinoid seed treatments in multiple crops (cotton, corn, soybeans, etc.) are believed to be the cause of resistance in *F. fusca*. (Huseth et al. 2016). Susceptibility of thrips to neonicotinoid insecticides varies depending on geographic location. Texas has relatively susceptible populations compared with other states and populations within each state vary widely in their susceptibility to neonicotinoids. Populations range from 5 to 55 fold resistant to neonicotinoids in Mississippi, and sensitive and resistant populations are found relatively near to one another (Huseth et al. 2016). Both thiamethoxam and imidacloprid (4A) (IRAC 2017) both share the same mode of action as neonicotinoids. Cross resistance between the compounds is possible.

Southeastern cotton growers need pest management options other than neonicotinoids for sustainable management of tobacco thrips in cotton.

Other control options available to farmers are unattractive for various reasons. Acephate applied foliarly is effective at controlling thrips but growers are hesitant to adopt acephate treatments in-furrow because they are linked to secondary pest infection of spider mites. Spider mites are primary and secondary pests in cotton. Spider mites are primary pests since they naturally infest cotton even without application of insecticides, but can be a secondary pest in that they are more likely to infest cotton treated with an in furrow or foliar treatment of acephate. Foliar application of acephate and pyrethroids are both linked to secondary pests, such as aphids and spider mites and foliar application for thrips requires careful timing (Jones et al. 2015). Along with its low secondary pest infestation, aldicarb is a key chemical rotation with neonicotinoids for control of tobacco thrips, especially in nematode prone soil which is prevalent in the southeastern United States. Neonicotinoids, the remaining effective control of tobacco thrips and other thrips species, is also in danger of a phase out despite scientific data. Data from numerous studies suggest minimal linkage between neonicotinoids and bee population decline (Nguyen et al. 2009, Blacquiere et al. 2012, Cresswell et al. 2012) and others give alternative reasons for honey bee population declines (Ellis et al. 2010, Johnson et al. 2010). Because EPA regulations stipulate that no previously registered product can be unregistered without evidence of harm to the environment, (Jensen 2015), imidacloprid, thiamethoxam, clothianidin, and acetamiprid (all neonicotinoids) are still registered with the EPA for use in cotton. Although, neonicotinoid control options remain in place

currently, alternative options should be investigated to mitigate the risk of loss of chemical control options for thrips. For long-term sustainability of thrips management in cotton, alternative management tactics supplemented by chemical control are necessary.

Biological control

Biological control of thrips, even in controlled settings, such as greenhouses, is difficult. Tobacco thrips occupy many niches in an ecosystem. The wide variety of niches makes the use of a single predator to control thrips difficult. Thrips eggs are deposited in plant tissue (Moritz 1997), and immatures occupy small crevices. Habits of pupation vary within the same species (Grout et al. 1986). When relative humidity is below 80%, western flower thrips pupate in the soil, but when relative humidity is high, a higher percentage pupate on their host plant (Holmes et al. 2012). This has implications for soil borne predators and entomopathogenic fungi that are popular biological control choices for insects dwelling, at least temporarily, in the soil. Although challenges exist to successfully implement a commercially viable biological control program for thrips, thrips have numerous natural enemies. Some of the potential *Heteropteran* predators of tobacco thrips include *Dicyphus tamaninii* (Wagner) (Albajes et al. 1996), damsel bug, *Nabis alternatus* (Parshley) (Taylor 1949), and minute pirate bug, *Orius* spp. (Wolff) (Tommasini and Nicoli 1996). Successful biological control of light, medium, and heavy populations of *F. occidentalis* is possible with mass release of *Orius insidiosus* (Wolff) (Van den Meiracker and Ramakers 1991). Larval parasitoids include *Ceranisus* spp. (Walker) (Bouček 1976). In laboratory settings, parasitism by *C. menes* on *T. tabaci* can reach 80% (Loomans and Pakozdi 1996). One species of egg parasitoid *Megaphragma*

(Timberlake), which uses *Frankliniella liliivora* (Kurosawa) as a host, could be capable of parasitizing tobacco thrips (Rao 1969). Despite the availability of biological control options, most use of biological control in field crops results in inadequate control (Gonzalez et al. 1992). Biological controls are important for assisting with control of thrips, but they alone are not enough to eliminate pest problems, especially in field crops.

Physical/mechanical barrier

Besides chemical control and biological control, physical barriers inhibiting thrips infestations are also used in pest management. Aluminum-surfaced mulch used in tomato fields reduced the incidence of thrips by 68% (Greenough et al. 1990). Although the effectiveness of mulch wanes once plant growth covers the mulch, cotton's primary window of sensitivity to thrips is during the early growing season (Gaines 1934). Reflective plastic aluminized polyethylene deterred thrips when placed on leeks (Benoit and Ceustermans 1990). Researchers found that physical barriers placed around fields were either negligible at stopping their infestation of the crop (Yudin et al. 1991) or increased the infestation (Lewis 1970, Lewis 1973). Authors believe barriers may stop airborne thrips which would otherwise be able to pass through an area unimpeded (Lewis 1970). The use of mechanical barriers could be an effective control for thrips as long as the value of the crop is high enough to justify the application of said physical barriers.

Reproductive control

Release of sterile individuals (Knipling 1970, Benedict and Robinson 2003) has potential to reduce populations of insects significantly. The Mediterranean fruit fly, *Ceratitis capitata* (Weidemann), and screwworm, *Cochliomyia hominivorax*

(Coquerel), were both reduced on continental levels with sterile individual release techniques (Krafsur 1998). In the case of thrips, which mate multiple times (Terry 1997) with different partners (Terry 1997) or produce offspring without the need for sexual reproduction (Terry 1997), releasing sterile individuals would have virtually no effect on reducing thrips densities. No authors mention the release of sterile individuals in thrips because thrips are not a good candidate for mass release of sterile individuals. Thrips produce viable males without sexual reproduction so release of sterile males theoretically would not stop successful production of new viable males.

Regulatory control/quarantine

While most regulatory controls are the domain of the federal government, there are some quarantine and regulatory practices that individual grower's practice that demonstrate effective thrips management. In glasshouse production, housing existing plants in houses apart from newly arrived plants is critical to hindering the spread of thrips (Parrella 1997). Irradiation as a quarantine measure is also a possibility in glasshouses (Bhuiya et al. 1999). Quarantine measures for cotton are difficult. Cotton is grown outdoors and screening fields of thousands of acres is not feasible or desirable. The lack of long-range pheromones for attracting tobacco thrips makes eradication difficult because some specimens would undoubtedly escape. Tobacco thrips also have a wide host range (Cho et al. 1995b). Other control measures are available that effectively reduce thrips populations more effectively than regulatory control.

Cultural control

Cultural controls include some of the best potential for sustainable control of insects, especially those that have a wide host range, such as tobacco thrips. Cultural control consists of utilizing alternative crop rotation, proper sanitation of fields, tillage, trap cropping, alternative planting dates, and host plant resistance to limit damage to crops or reduce pest populations. Other examples of successful cultural control of insects are numerous (Hokkanen 1991).

Crop rotation is important for the control of insects, especially insects that cannot move long distances or cannot overwinter in other crops (Kettunen et al. 1988, Sexson and Wyman 2005). While thrips can travel relatively long distances for their size and overwinter in other crops nearby in regions where they are pests, crop rotation has been proven to reduce susceptibility of cotton to thrips. Cotton planted following canola, *Brassica napus* (L.), has more adult and immature thrips than cotton planted following wheat, *Triticum* spp. (L.), or in fallow fields (All et al. 1993). Another study examined thrips damage in cotton planted every year, cotton and corn planted in alternating years, and cotton planted every year with a rye, *Secale cereale* (L.), cover crop. The study found that crop rotation only had an impact on thrips damage to cotton when conservation tillage was used and when aldicarb was not available (Bauer et al. 2005). When conventional tillage was used, the effect of crop rotation on thrips was less pronounced (Bauer et al. 2005). When aldicarb was available, the effect of crop rotation on thrips was less pronounced (Bauer et al. 2005). Another crop rotation technique blends the end of winter crop with the beginning of a summer crop. Reduced populations of thrips were

observed in cotton planted in standing wheat two to three weeks before wheat harvest (Greene et al. 2015).

Like crop rotation, the impact of tillage on populations of thrips population and damage to cotton is dependent on other factors. Populations of thrips in seedling cotton are lower under strip-till methods compared with conventional tillage (Griffin et al. 2010). Authors relate this to the comparatively increased ground cover characteristic of strip till systems in relation to conventional tillage (Griffin et al. 2010). Assuming ground cover is the main driver reducing thrips infestation, cover crops and tillage techniques that provide cotton the most cover without disrupting its growth are the best choice (Roberts and Brown 2004). Tillage is only as effective as the cover crop that the tillage conserves (All et al. 1993). Populations of thrips are lower in cotton planted after canola, wheat, and fallow fields that utilize a no-till system compared with conventional tillage systems (All et al. 1993). In general, researchers associate conventional tillage with a higher risk of infestation than conservation tillage (Roberts et al. 2012).

Tobacco thrips are shown to overwinter primarily on host plants and not in the soil (Cho et al. 1995b, Groves et al., 2002). This indicates that elimination of weeds and host plants that tobacco thrips overwinter in around cotton production areas could lead to smaller populations of tobacco thrips in spring. Researchers generally conclude that sanitation of winter crop residue before planting cotton in the southeastern United States results in higher thrips damage and thrips populations (Roberts et al. 2012, Greene et al. 2015). Winter crop residue deters weed establishment (Bond and Grundy 2001), although

effects of winter weed mass near cotton fields on subsequent thrips infestation is unknown.

Trap cropping

Trap cropping tobacco thrips is less widespread than other cultural controls. No studies exist examining the effect of flowering plants placed in cotton field borders or other locations near cotton field on the effect of tobacco thrips damage to cotton. To be effective, flowering weeds would need to be a color that attracts tobacco thrips. White plastic and gold or blue aluminum foil attract thrips that infest seedling cotton in the southeastern United States, although species were not identified in the study (Beckham 1969). Other researchers suggest that tobacco thrips do not have a color preference (Cho et al. 1995a), although only blue and yellow colors were tested. Regardless of the color preference of tobacco thrips, any weeds utilized as a trap crop have the potential to serve as a windbreak that stops thrips riding wind currents or other movements and allows them to infest nearby crops (Lewis 1970), although finding a weed or other suitable candidate would likely also have other negative consequences.

The effect of planting date can have a significant impact on thrips infestation in cotton (Micinski et al. 1990). Planting early in African cotton production is commonplace. Crops planted early have more time to establish. Established cotton crops withstand thrips infestation better than young cotton crops (Parrella and Lewis 1997). In the southeastern United States, cotton planted late is generally thought to fare better against thrips infestations (Roberts et al. 2012). Cotton planted and grown under the warm conditions of late plantings dates grows faster and has better stand establishment

(Micinski et al. 1990). Cotton planted later grows exponentially faster than early planted cotton to such an extent that late planted cotton may reach the same stage of development as cotton planted earlier in the season (Herbert et al. 2010). Faster growing cotton gives thrips less time to colonize it during the sensitive seedling stage. Systemic insecticidal treatments are more effective in cotton planted later (Jones et al. 2015). Planting date plays an even larger role in cotton that does not have access to enough moisture (Micinski et al. 1990). Drought stressed cotton is more sensitive to thrips injury. Planting date is an effective tool, but cotton has a limit to how late it can be planted. Cotton that is planted too late grows more vegetation in relation to fruit (Cathey and Meredith 1988), and is exposed to late-season pests for a longer period of time (Lambert et al. 1996). Planting date has interactions with the variety of cotton planted that are important to note.

Early maturing varieties of cotton are less likely to be affected by the negative effects of later planting dates. Early maturing varieties of cotton are generally more capable of recovering from early thrips damage (Johnson et al. 1989). Other than interactions variety has with planting date, the variety of cotton has intrinsic effects on populations of thrips. Cotton cultivars with hairy lower leaf surfaces are thought to suffer less from thrips than glabrous varieties (Wardle and Simpson 1927, Zareh 1985), but other authors report that glabrous leaves result in fewer thrips (Zareh 1985, Leigh 1995).. Although, the relationship between cotton variety and thrips densities and damage is more complex than hairy versus smooth cultivars. A cotton variety resistant to western flower thrips (Trichilo and Leigh 1988) is the result of a chemical that occurred in the leaves of cotton but not in the pollen. The variety resistant to thrips (*Frankliniella*

occidentalis) was also resistant to spider mites (*Tetranychus urticae*) (Trichilo and Leigh 1988). Testing varieties for resistance is complex. Thrips have two modes of feeding. One characterized by many short shallow probes and another with few long, deep probes (Harrewijn et al. 1996a, Harrewijn et al. 1996b). Sakimura (1963) observed that thrips tended to feed more shallowly under field conditions compared with laboratory conditions. In resistant cultivars of tomato, western flower thrips only feed on the epidermal cells of the plant, but feed on the mesophyll and epidermal cells of susceptible cultivars (Krishna Kumar et al. 1995). Thrips feeding shallowly on resistant cultivars in the field might prevent them from ingesting or contacting harmful chemicals in the mesophyll of the plant that they come into contact with in the lab. No information is known on differences in feeding depth between adult and immature thrips.

Integrated Pest Management

The goal of an IPM program is not elimination of chemical controls, but a more effective use of chemical controls utilized in conjunction with other controls. For example, chemical controls such as seed treatments are more effective in planting dates after May 20 in South Carolina (Jones et al. 2015). Varietal selection plays a role in the ability of cotton to recover from early season thrips damage (Johnson et al. 1989). Tillage and crop rotation both influence the population of thrips infesting seedling cotton (All et al. 1993, Bauer et al. 2005).

CHAPTER TWO

EFFECTS OF PLANTING DATE ON THRIPS (THYSANOPTERA THIRIPIDAE IN COTTON

Introduction

Thrips (Thysanoptera: Thripidae) are prolific and consistent pests of seedling cotton, *Gossypium hirsutum* L., in the United States (Burris 1980, Reed 1988, Reay-Jones et al. 2017), where they feed on the epidermal and mesophyll cells of host plants (Wardle and Simpson 1927, Chisholm and Lewis 1984). Excessive feeding from thrips leads to terminal malformation in seedling cotton plants, abnormal growth, or, in extreme cases, the death of the terminal growing point of the plant (Reed 1988). Under severe infestations, thirty to fifty percent yield loss in cotton can occur (Cook et al. 2011). Systemic insecticides (mainly thiamethoxam, imidacloprid, and acephate) applied as seed treatments or in-furrow use of granular or liquid insecticides are commonly used at planting to control infestations of thrips in seedling cotton in the United States (Cook et al. 2011). However, loss of key chemical options for management of thrips have made alternative control options necessary for management of thrips in the southeastern United States.

Aldicarb was a key tool for management of thrips because of its effectiveness across a wide range of conditions (Plain et al. 2002), but insufficient quantities of the product in recent years have forced cotton producers to rely on other control options. Without aldicarb, chemical rotations and resistance management for thrips have been hampered. The predominant species of thrips infesting cotton, tobacco thrips,

Frankliniella fusca Hinds, has developed widespread, yet variable, resistance to thiamethoxam and imidacloprid (Huseth et al. 2016). These neonicotinoid insecticides, primarily used as seed treatments, are some of the few remaining chemical tools available to manage thrips in cotton in the United States. Other chemical options available for thrips include acephate and phorate.

Thrips commonly infest cotton throughout the season; however, their primary window of economically significant infestation occurs during the seedling stage, which is the stage of cotton development that they are most susceptible (Dunham and Clark 1937, Reay-Jones et al. 2017). Populations of thrips that cause injury to cotton typically emigrate from surrounding landscapes into cotton fields in large numbers and successfully colonize seedling cotton in a short period (Burris 1989). Studies suggest that spring dispersal of *F. fusca* from weeds and winter crops is based primarily on temperature, precipitation accumulation, natural senescence of seasonal changes, purposeful termination of a crop for harvest, and number of days of precipitation, the timing of which is predictable with a reasonable degree of certainty with degree day models (Morsello et al. 2008). The benefits of a model that can determine risk of thrips injury is useful because it may facilitate more widespread use of alternative control options for thrips. This is especially important because alternative methods for controlling thrips are needed due to the lack of chemical control options. Planting date is a good candidate as a management tool for thrips because the window of susceptibility of cotton to thrips is only a few days long under favorable conditions for cotton growth. Authors have noted the use of planting date as a cultural practice that is potentially useful to avoid peak

populations of thrips (Slosser 1993, Parajulee et al. 2006). In a study in Texas, cotton planted in late June had lower numbers of thrips infestations compared with cotton planted in April (Slosser 1993). In another study, thrips were more prevalent in cotton planted timely (second week of May) than in late-planted (second week of June) cotton, but the findings did not indicate whether the thrips infestations resulted in damage or yield loss (Parajulee et al. 2006). Although previous studies have examined the potential of different planting dates to manage thrips in cotton, a study with a greater resolution and range of planting dates compared with the two (Parajulee et al. 2006) and three (Slosser 1993) planting dates used in previous studies is needed to provide more information on the potential for different planting dates to manage thrips in cotton. The objectives of this study were to examine the effects of ten planting dates from mid-April to mid-June on density of thrips, feeding injury by thrips, plant growth, and yield of cotton.

Materials and methods

Trials were located at the Clemson University Edisto Research and Education Center in Blackville, SC, in 2015, 2016, and 2017 (Table 2.1). In 2015, seed from variety DP 1137 B2RF (Monsanto Company, St. Louis, MO) were treated commercially with either imidacloprid (0.375 mg/seed; Gaucho, Bayer CropScience, Research Triangle Park, NC) and fungicides, or fungicides only. In 2016, seed from PHY 333 WRF (Dow AgroSciences, Indianapolis, IN) were treated commercially with either imidacloprid and thiodicarb (each AI at 0.375 mg/seed; Aeris, Bayer Crop Science) and fungicides, or with fungicides only. In 2017, seeds from varieties PHY 333 WRF and PHY 499 WRF (Dow

AgroSciences) were either treated with a fungicide alone or received at planting an additional in-furrow application of phorate (Thimet, Amvac Chemical, Newport Beach, CA) at 5.6 kg AI/hectare. Split-plot designs were used in 2015 and 2016, with planting date as the main plot treatment and insecticide as the subplot treatment. A split-split plot design was used in 2017, with planting date as the main plot treatment, insecticide as the subplot treatment, and variety as the sub-subplot treatment (Table 2.1). Plots were 12.2 meters long (40 feet) and 7.72 meters (25.3 feet) wide. Row spacing was 96.5 centimeters (38 inches) with three seeds planted per 30.4 centimeters (1 foot). Four replications were included in each trial.

Table 1.1. Year, locations, planting date, cotton variety and at-plant insecticide in field trials in South Carolina.

Year	Location	Variety	Insecticide	Planting dates
2015	Blackville, SC	DP 1137 B2RF	0.375 mg imidacloprid/seed	15, 24 April; 1, 8, 15, 21, 29 May; 5, 12, 19 June
2016	Blackville, SC	PHY 333 WRF	0.375/mg/imidacloprid/seed & 0.375/mg/thiodicarb/seed (Aeris)	18, 25, 29 April; 5, 12, 17, 26 May; 3, 10, 15 June
2017	Blackville, SC	PHY 333 WRF & PHY 499 WRF	5.6 kg/phorate/hectare	12, 21, 27 April; 4, 12, 17, 26, 31 May; 9, 14 June

Data collection

Densities of thrips were measured using a destructive sampling technique where ten randomly selected cotton plants were pulled by hand from each plot, five from row two and five from row seven. After each plant was removed from the ground, it was immersed quickly and individually in a 1-liter jar of 50% isopropyl alcohol in the field to dislodge thrips from plants into the alcohol. Once the samples were returned to the laboratory, jar contents (alcohol and thrips) from a plot were poured onto # 8 filter paper (Fisher Scientific, Waltham, MA) with a fast flow rate and coarse porosity. To accelerate the process of filtration in the laboratory, filtration procedures (Burriss et al. 1990) were modified to accommodate field washing of plant samples by including Buchner funnels attached to an electric pump operating at a range of 0.7 to 3.4 bars. After filtration, numbers of adult and immature thrips on each filter paper were counted with dissecting microscopes. Injury ratings were estimated visually according to Hawkins et al. (1996) but modified to a general visual rating of plants representing the entire plot. Injury ratings used a 0-5 scale (Figure 1.1), where '0' represented no indication of feeding injury from thrips, and '5' indicated the most severe injury, which included severely stunted plants and curling of true leaves, death of the terminal growing point of the plant, or death of the plant. Injury ratings were taken as often as thrips samples were taken for each site when possible. Heights from the soil to the terminal growing point were measured for five plants per plot randomly selected among rows three, four, five, and six. Plant heights were recorded from the time of emergence every time that thrips were sampled, which occurred for four weeks at the majority of locations. While

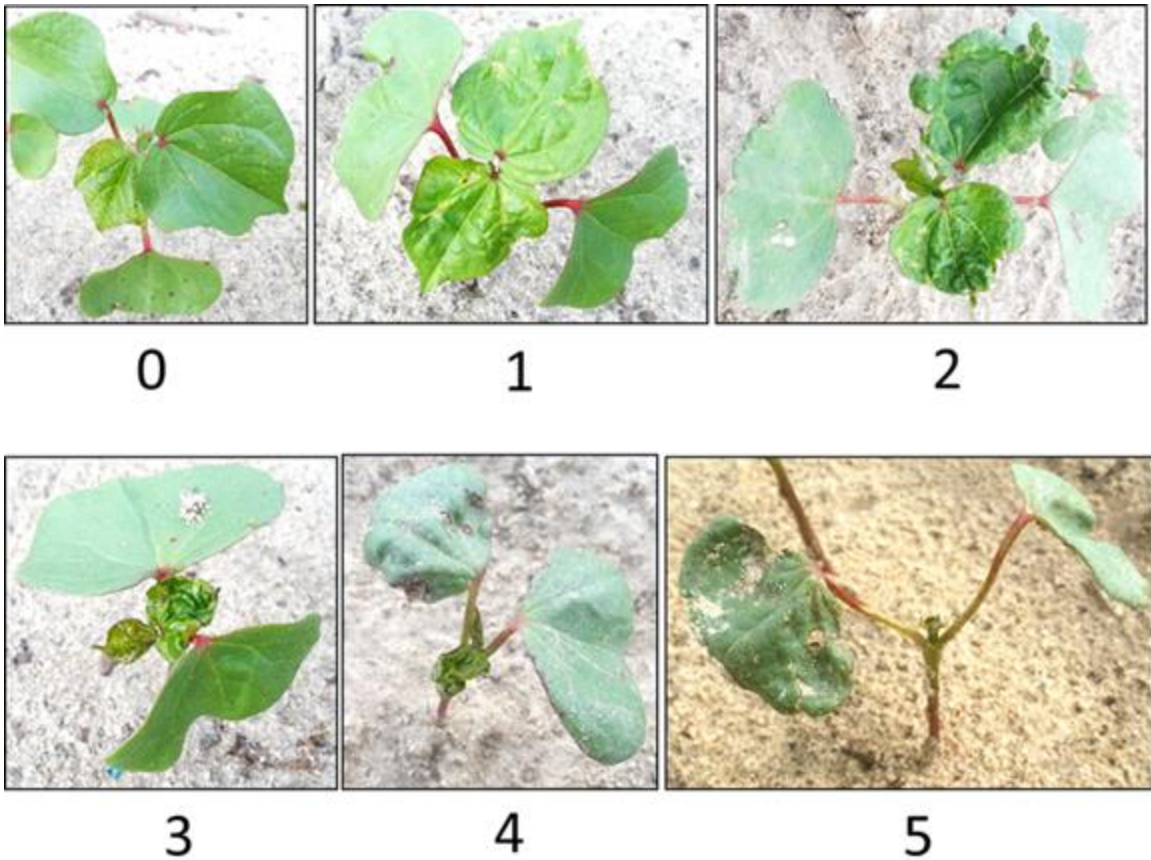


Figure 1.1 Example visual injury rating scale used in this study

differing planting dates, agronomic characteristics of varieties, and environmental conditions meant that growth stages did not match up across locations or within plots exactly, all locations recorded three different plant height measurements, one at the cotyledon/one true leaf stage, the second at the two true leaf/three true leaf stage, and a third at the four/five true leaf stage. A plant height measurement was also taken at forty-two days after planting. Dry weight biomass was measured at forty-two days after planting by excising at the soil line five plants per plot randomly selected among rows three, four, five, and six and placing them into drying ovens at 71°C for 48 hours before

being weighed. Yields of seed cotton were determined from the middle four rows of each plot with a mechanical plot picker.

Data analyses

In 2015 and 2016, thrips densities, injury ratings, dry weights, and seed cotton yields were analyzed using a two-way analysis of variance as a split-plot design with planting date, insecticide treatment, and their interaction as fixed effects and replicate and replicate x planting date as random effects (Littell et al. 2006; PROC MIXED; (SAS Institute 2015). Means for all variables were pooled across all collection dates. Means were separated using Tukey's HSD (Tukey 1953). Degrees of freedom were adjusted using the Kenward-Roger method (Kenward and Roger 1997). Thrips-days were calculated using averages of adult and immature thrips at each sampling date (Ruppel 1983). The number of adult and immature thrips between each pair of consecutive samples for each planting date were averaged together and then multiplied by the number of days between each pair of samples. The number of thrips days for each pair of consecutive pair of samples for each planting date were added together to get the final thrips-days value used in this study

In 2017, thrips densities, injury ratings, dry weights, and seed cotton yields were analyzed as a three-way analysis of variance in a split-split plot design, with planting date, insecticide treatment, variety, and their interactions as fixed effects and replicate and replicate x planting date and replicate x treatment interactions and replicate x variety interactions as random effects (Littell et al. 2006, SAS Institute 2015). Means were separated using Tukey's HSD (Tukey 1953).

Because data for all variables across all years of the study showed some evidence of non-normality, analyses of variances were conducted on both rank transformed (RT-1) data and untransformed data using the same models, with the RT-1 transformed data not having a distribution (Conover and Iman 1981). For all variables, results indicated that the RT-1 transformation did not alter the significance of fixed effects or means . Furthermore, the distribution of the transformed data was not altered compared with the untransformed data. The non-normality of the data was, therefore, not deemed sufficiently important to consider using the RT-1 transformation.

Results

Adult Thrips - Cotyledon

Planting date had a significant effect on adult thrips at the cotyledon stage in 2015, 2016, and 2017 (Table 1.2). In 2015, untreated cotton planted in late May (29 May) had 5.8-fold fewer adult thrips than cotton planted in early May (8 May; Figure 1.2). In 2016, untreated cotton planted on 10 June had 7.4-fold fewer adult thrips than untreated cotton planted on 12 May (Figure 1.2). Cotton planted on 18 April in 2016 also had low densities of thrips, which were not significantly lower than cotton planted on 12 May. In 2017, cotton planted after mid-May (26 May) had 8.0-fold lower numbers of adult thrips than cotton planted on 27 April (Figure 1.2).

Seed treatments of insecticide resulted in significantly reduced numbers of adult thrips present on cotyledon cotton in 2015 and in 2016, but not in 2017 (Table 1.2). Treatment with imidacloprid in 2015, averaged across planting dates, lowered the number of adult thrips 1.8-fold compared with untreated plots. In 2016, treatment of Aerial (imidacloprid + thiodicarb) reduced the number of adult thrips 2.6-fold. The significant interaction of planting date and treatment in 2015 was due to the only difference within a planting date between treatments occurring with the 1 May planting date (Figure 1.2).

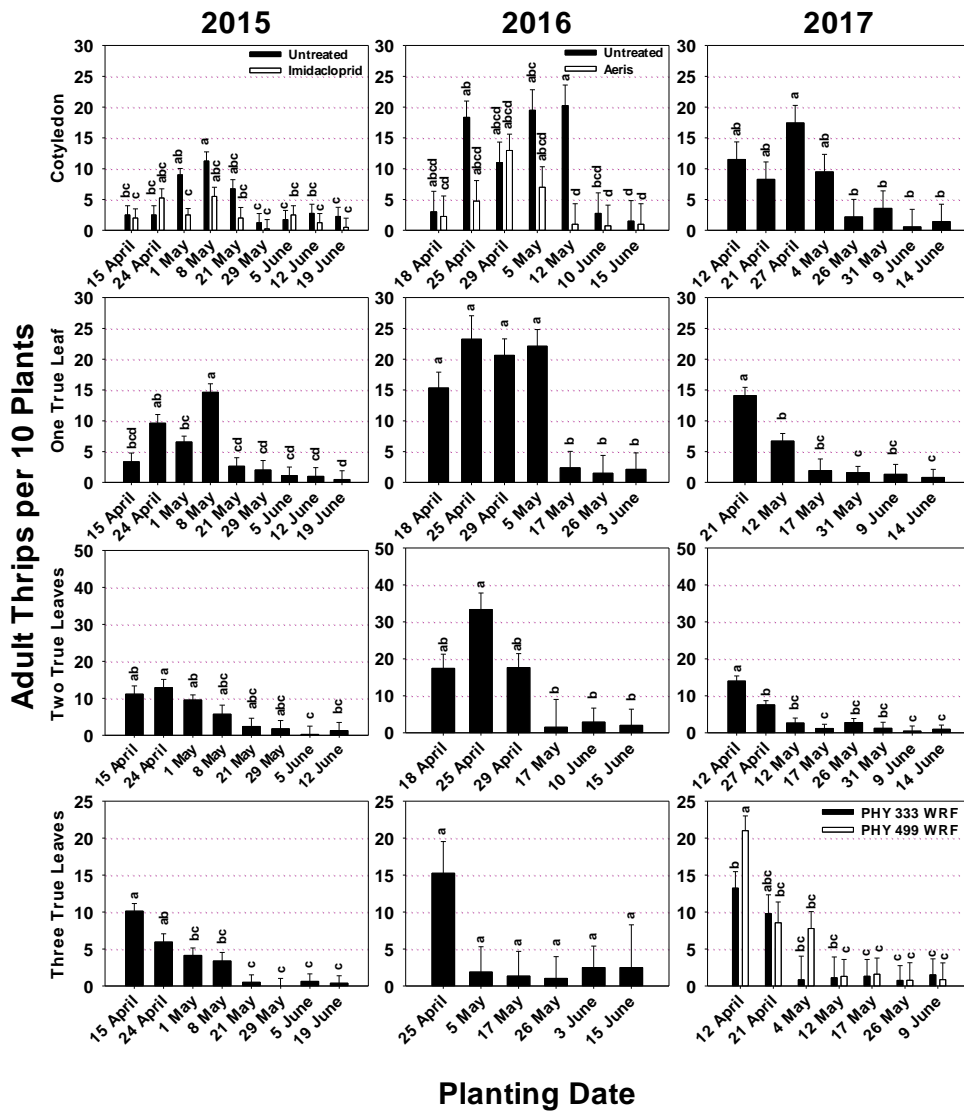


Figure 1.2 - Adult thrips density at four cotton seedling growth stages.

The significant interaction of planting date and treatment in 2016 was due to Aerial reducing the number of adult thrips 20.3-fold at the 12 May planting date, while the seed treatment was generally less effective at other planting dates (Figure 1.2). Differences between planting dates were subtle for adult thrips at the cotyledon stage in 2017, with only the 27 April planting date having more thrips than planting dates after 4 May.

Adult Thrips – One True Leaf

At the one true leaf stage, planting date had a significant effect on adult thrips in 2015, 2016 and 2017 (Table 1.2). In 2015, cotton planted on or after 21 May generally had fewer thrips than earlier planted cotton, with 3.7-fold more adult thrips on 24 April than on 21 May (Figure 1.2). In 2016, thrips densities decreased in cotton planted after 5 May (Figure 1.2). In 2017, adult thrips peaked in cotton planted on 21 April, followed by a gradual decline (Figure 1.2). Insecticide significantly reduced the number of adults at this stage 3.9-fold in 2016, but not in 2015 and 2017, although there was no planting date by insecticide interaction (Table 1.2).

Adult Thrips – Two True Leaves

At the second true leaf growth stage, planting date had a significant effect on adult thrips in 2015, 2016, and 2017 (Table 1.2). In 2015, cotton planted in June had fewer adult thrips than cotton planted on 24 April (Figure 1.2). In 2016, cotton planted on 25 April had significantly more adult thrips than cotton planted in May and June (Figure 1.2). In 2017, adult thrips generally declined with planting date.

Adult Thrips – Three True Leaves

At the three true leaf stage, planting date had a significant effect on adult thrips in 2015 and 2017, but not in 2016 (Table 1.2). Densities of adult thrips were significantly lower on cotton planted on or after 21 May than on cotton planted in April (Figure 1.2). In 2017, planting cotton in May and June rather than mid-April resulted in reduced numbers of adult thrips (Figure 1.2). A significant interaction was detected between planting date and variety (Table 2.2), with more adult thrips on PHY 499 WRF compared with PHY 333 WRF on 12 April, but not for other planting dates.

Immature Thrips - Cotyledon

The number of immature thrips found on cotyledon cotton were significantly affected by planting date in 2015 and in 2017, but not in 2016 (Table 1.3). The interactions of planting date and insecticide treatment were significant in 2015 and 2017. In 2015, densities of immature thrips were lower in untreated cotton planted in May and June, compared with cotton planted during April (Figure 1.3); immature thrips in treated plots did not vary with planting date. In 2017, untreated cotton planted in May and June also had reduced immature thrips compared with untreated cotton planted in April (Figure 1.3); immature thrips in treated plots did not vary with planting date.

Immature Thrips – One True Leaf

At the first true leaf growth stage, the number of immature thrips was significantly affected by planting date in 2015 and 2017, but not in 2016 (Table 1.3). In 2015, densities of immature thrips were generally lower in cotton planted in late May and June compared with cotton planted on 8 May (Figure 1.3). In 2017, cotton planted on 21 April had higher numbers of immature thrips than cotton planted on 12 May and 14 June (Figure 1.3). The effect of insecticide was significant in 2015, 2016, and 2017 at the one true leaf stage. In 2015, treatment with imidacloprid reduced immature thrips 2.9-fold. In 2016, treatment with Aeris (imidacloprid + thiodicarb) reduced immature thrips 3.9-fold. In 2017, the interaction of planting date and treatment was significant; however, once the conservative Tukey mean separation tests were used, no differences were detected between treated and untreated plots within any single planting date (Table 1.3).

Immature Thrips – Two True Leaves

At the second true leaf growth stage, immature thrips varied significantly with planting date in 2015, 2016, and 2017 (Table 1.3). In 2015, immature thrips in untreated plots were 6.6-fold greater in plots planted on 1 May (40.4) compared with plots planted on 21 May (6.1) (Figure 1.3). In 2017, immature thrips were greater for the 12 April planting date compared with all other dates (Figure 1.3). Insecticide treatment affected the number of immature thrips averaged across all planting dates in 2016 and 2017, but not in 2015 (Table 1.3). The interaction between planting date and treatment in 2016 was caused by a lack of planting effect in treated plots, whereas untreated plots of cotton planted on 10 June had 92.6-fold fewer immature thrips than cotton planted on 25 April (Figure 1.3).

Immature Thrips – Three True Leaves

Planting date significantly affected the number of immature thrips sampled in 2015, 2016, and 2017 at the third true leaf stage (Table 1.3). In 2015, immature thrips peaked at the 15 April planting date and declined in May and June (Figure 1.3). A similar trend was observed in 2016, with immature thrips peaking on 25 April (Figure 1.3). In 2017, densities of immature thrips were low overall but generally declined after mid-May (Figure 1.3).

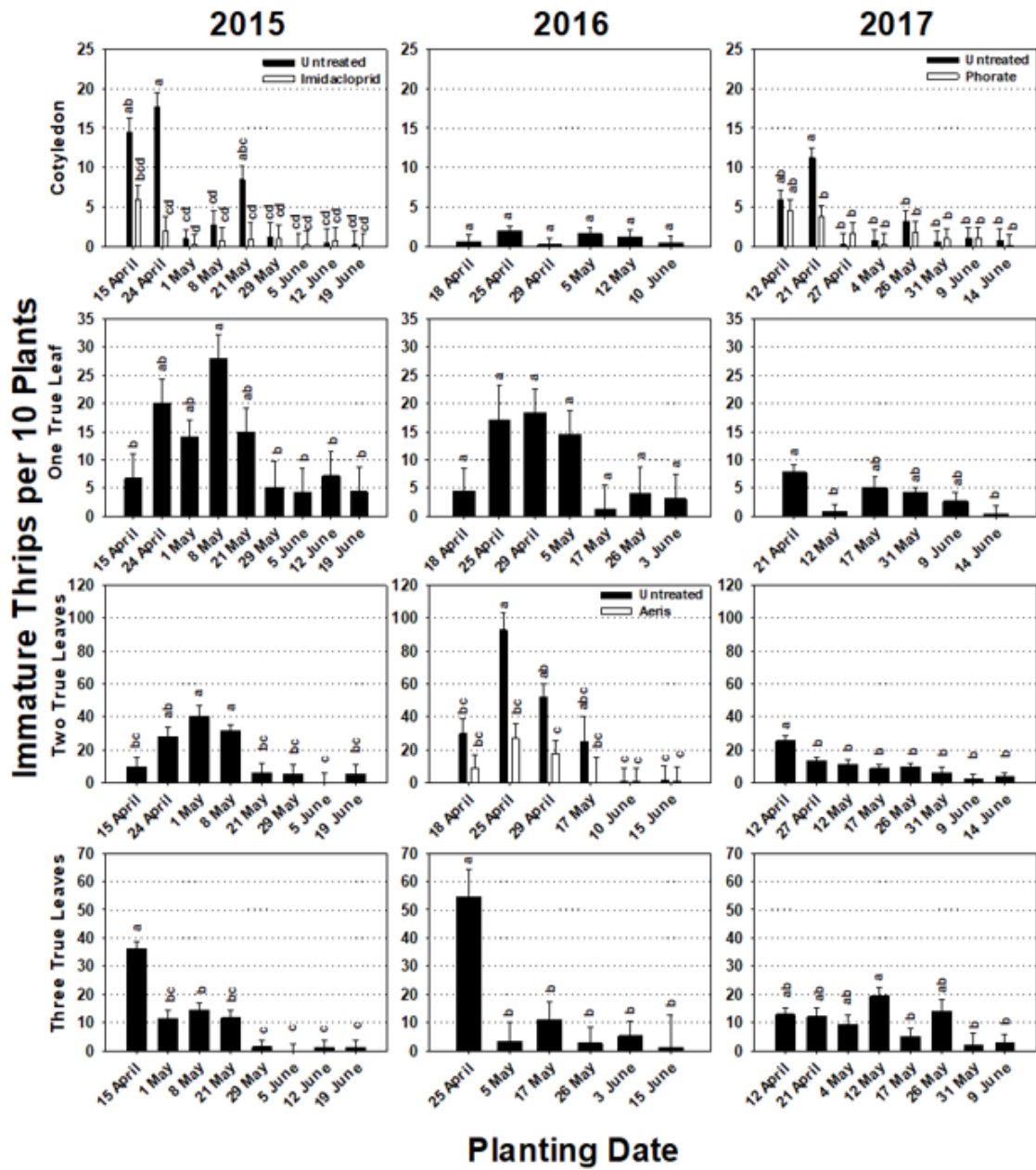


Figure 1.3 – Immature thrips density at four cotton seedling growth stages.

Cumulative Thrips-Days

For cumulative thrips-days in 2015, the effects of planting date and treatment (imidacloprid) were both significant, but their interaction was not (Figure 1.4). Cotton planted on 8 May and 21 May had significantly different cumulative thrips-days of 539.8 and 186.8, respectively (Figure 1.4). Imidacloprid seed treatments significantly reduced cumulative thrips-days 2-fold in 2015, from 301.2 in untreated plots to 150.8 in treated plots.

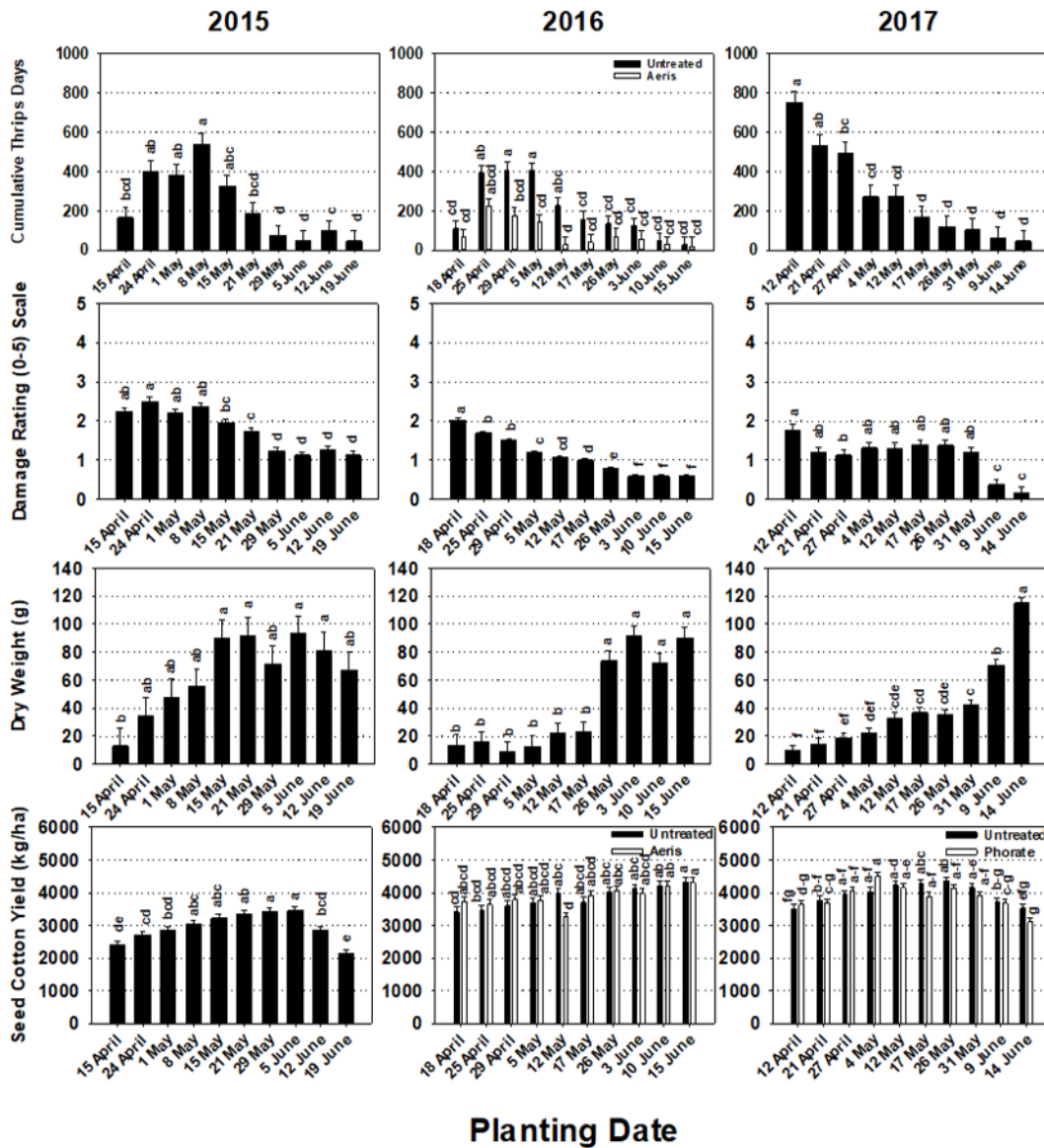


Figure 1.4 – Cumulative thrips days, injury rating, dry weight, and seed cotton yield.

In 2016, the planting date and treatment interaction (imidacloprid + thiodicarb) significantly altered the number of cumulative thrips-days. Delaying planting date from 5 May to 26 May reduced cumulative thrips-days in untreated cotton 2.6-fold, from 405 cumulative thrips-days on 5 May to 156 cumulative thrips-days on 26 May (Figure 1.4). Plots treated with Aeris did not differ in the number of thrips-days between planting dates in 2016. Across all planting dates, insecticide treatment reduced cumulative thrips-days 2.4-fold in 2016.

In 2017, cumulative thrips-days were significantly affected by planting date and insecticide treatment, but not the interaction (Table 1.2). Cumulative thrips-days were significantly reduced for cotton planted on or after 17 May when compared with cumulative thrips-days for planting dates in April (Figure 1.4). Across all planting dates, phorate treatment significantly lowered cumulative thrips-days 1.5-fold

Thrips Damage Ratings

In 2015, both planting date and treatment (imidacloprid) significantly impacted damage ratings (Figure 1.4). Cotton planted on 21 May (rating of 1.7) had injury ratings 1.4-fold lower than cotton planted on 8 May (rating of 2.4) (Figure 1.4). Plots treated with imidacloprid had injury ratings 1.2-fold lower than plots left untreated in 2015, a reduction from 2.0 in untreated plots to 1.6 in treated plots.

In 2016, injury ratings varied significantly with planting date and insecticide treatment but not with the interaction (Table 1.2). Planting cotton on 17 May (rating of 1.0) compared with 5 May (rating of 1.2) reduced injury 1.2-fold (Figure 1.4). Cotton

treated with Aeris in 2015 reduced injury 1.2-fold when averaged across planting dates, from 1.2 in untreated plots to 1.0 in treated plots.

In 2017, both planting date and treatment significantly affected thrips injury ratings but not the interaction (Table 1.2). Cotton planted on 9 June (rating of 0.4) had injury ratings 3.2-fold lower than cotton planted on 31 May (rating of 1.2) (Figure 1.4). Averaged across planting dates, cotton with phorate treatment (rating of 1.3) had a 1.3-fold decrease in injury compared with untreated plots (rating of 1.0). A significant variety x planting date interaction was caused by injury being significantly greater on PHY 499 WRF on 31 May compared with PHY 333 WRF.

Dry Weight Biomass

In all years, only planting date significantly affected biomass. In 2015, the first date (15 April) exhibited a lighter weight than four planting dates in May and June (Figure 1.4). In 2016, greater weights were found in planting dates after mid-May (73.9 g all five plants totaled on 26 May) compared with early-May (12.8 g on 5 May) (Figure 1.4). In 2017, dry weights of cotton planted after mid-May (35.1 g on 26 May) were 2.4-fold higher than cotton planted on 21 April (14.6 g) (Figure 1.4).

Seed Cotton Yield

Planting date had a significant effect on seed cotton yield in all years. In 2015, cotton planted on 21 May (3,323.8 kg/ha) had 1.2-fold higher yield than cotton planted on 24 April (2,707.6 kg/ha) (Figure 1.4). In 2015, insecticide did not affect cotton yield. In 2016, untreated cotton planted on 15 June (4,340.6 kg/ha) had yields 1.2-fold higher than untreated cotton planted on 25 April (3,463.5 kg/ha) (Figure 1.4). In 2016, cotton

generally yielded as high as its untreated counterpart, and only significantly affected yield on 12 May (Figure 1.4). In 2017, yields were affected by planting date and the planting date x variety interaction (Table 1.2), with cotton planted in May generally having higher yields than cotton planted in April or June (Figure 1.4). When the conservative Tukey means separation tests were applied to the interaction between planting date and variety in both 2016 and 2017, no significant differences were detected between treatments based on planting date.

Discussion

For all years (2015-2017), seedling cotton at all growth stages supported higher densities of adult and immature thrips in cotton planted before mid-May than in cotton planted after mid-May. The predominant species was likely *F. fusca*, based on data from plots at the same location and dates (Reay-Jones et al. 2017, Wang et al. 2018). These results were consistent with those obtained by (Slosser 1993), who demonstrated the negative influence of progressive planting date on thrips (primarily western flower thrips, *Frankliniella occidentalis* Pergande) on cotton in Texas. Results from another study in Texas indicated that densities of thrips were significantly lower in late-planted (15 June) cotton when compared with timely (15 May) planted cotton (Parajulee et al. 2006).

In our study, thrips-days more succinctly represented densities of thrips across growth stages and showed the progressive influence of planting date on thrips. Although densities of thrips and thrips-days were generally reduced by delaying planting to after mid-May, abundance of thrips was also low on cotton planted on the earliest dates in mid-April during 2015 and 2016. During these two years, densities of thrips were lower

compared to 2017, likely because of lower temperatures that occurred before cotton was planted. For example, the accumulation of degree days (Wilson and Barnett 1983) calculated from 1 January to 30 April was 443.4, 562.4, and 638.1 in 2015, 2016, and 2017, respectively, when using a base development threshold of 10.5°C (Lowry et al. 1992, Morsello et al. 2008) for *F. fusca*. Thrips grow more quickly and spend more time above their development threshold when temperatures are relatively higher, while lower temperatures result in slower growth of thrips. In addition, total precipitation from 1 January to 30 April in 2015, 2016, and 2017 was 39.4, 30.8, and 31.8 cm, respectively. Rainfall can also have a significant impact on thrips dispersal by delaying the senescence of winter hosts for thrips (Morsello and Kennedy 2009), and the greater rainfall in 2015 could have affected thrips dispersal to cotton. The greater rainfall in 2015 allowed winter weeds to survive longer, and thus act as a host for thrips longer until they senesce and thrips dispersal begins. Once the infestation of the crop has begun however, rainfall is detrimental to thrips populations.

Our study showed that planting cotton after mid-May in South Carolina can result in reduced risk of injury from thrips infestations. However, delaying the planting date of cotton can result in excess vegetative growth (Cathey and Meredith 1988), especially for late-maturing varieties of cotton planted after 20 May (Jones et al. 2017). Although we did not include any late-maturing varieties in this study, PHY 499 WRF is a popular mid-to-late maturing variety that has similar recommended planting dates as for late-maturing varieties. Production recommendations for cotton in South Carolina suggest the use of plant growth regulators for cotton planted after 20 May to reduce excess vegetative

growth (Jones et al. 2017). As a result, growers must take into account the potential increased costs of growth regulator applications if selecting a late planting date to mitigate risk of injury from thrips. In addition to the expenses of plant growth regulation, growers should consider costs of late-season control of insects. Cotton planted after mid-May in South Carolina could be at an elevated risk for higher infestations or increased losses from bollworm, *Helioverpa zea* (Boddie) (Akin et al. 2011), and stink bugs (Heteroptera: Pentatomidae), as these species can be problematic in cotton delayed or planted later than usual. Although populations of bollworm in the southeastern United States have developed practical resistance to the *Bacillus thuringiensis* (Bt) toxin Cry1Ac expressed in transgenic cotton (Reisig et al. 2018), foliar applications of insecticide targeting bollworms are expected to decrease as adoption of cotton expressing Vip3Aa increases. This enhanced efficacy of cotton expressing Vip3Aa for bollworm should provide at least a short-term opportunity to delay planting to control thrips without undue risk of loss from late-season infestations of bollworm. Thrips management programs should carefully consider all potential side effects of a later planting date.

Of the at-plant options of insecticide included in this study, none consistently controlled thrips, including neonicotinoid seed treatments, likely because *F. fusca* has developed reduced susceptibility to the neonicotinoid insecticides imidacloprid and thiamethoxam (Huseth et al. 2016). The insecticide phorate did not consistently provide control of thrips either. While reintroduction of the carbamate aldicarb into thrips management programs could alleviate problems with resistance to neonicotinoid insecticides, cases of resistance to carbamates are already known in *F. occidentalis* (Gao

et al. 2012), further emphasizing the need for cultural control practices, such as alteration of planting date. Thrips can have multiple pathways of developing resistance to insecticides (Gao et al. 2012) with cross-resistance to insecticides from different classes, such as diazinon (organophosphate) and imidacloprid (neonicotinoid) in *F. occidentalis* (Zhao et al. 1995) through an enhanced metabolic mechanism (Gao et al. 2014). Other than at-plant options for thrips control, foliar treatments for thrips (typically acephate) are not only an additional cost for growers and more variable in their application depending on weather, but they can also result in outbreaks of two-spotted spider mite, *Tetranychus urticae* (Koch), in cotton (Trichilo and Leigh 1986, Smith et al. 2013).

Results of this study indicate that delayed planting of cotton, within an agronomically acceptable interval that does not result in reduced yield, can be as effective as chemical control of thrips, especially in areas where thrips populations evolved reduced susceptibility to insecticides. The results of this study indicate that the risk of injury from thrips in cotton generally declined with progressive dates of planting and that risk can vary considerably between years, which validates the need for a tool to help quantify risk temporally and spatially.

Finally, recent challenges for managing thrips in cotton in the United States reaffirm the importance of considering a cultural control tactic, such as delayed planting date, as a component of IPM to potentially reduce reliance on chemical control. Another promising option for the future includes a novel Bt event MON 88702 in cotton that expresses Cry151Aa2.834_16, with reported activity on thrips (Bachman et al. 2017). Although the toxin is effective in significantly reducing densities of and

feeding injury from thrips, it will not be available for commercial use for a number of years. Until new methods of management for thrips are available, sustainable production of cotton will need to rely on minimizing the use of insecticides by selecting a planting date using the Thrips Infestation Predictor for Cotton to avoid peak thrips pressure.

Table 1.2. ANOVA statistics for adult thrips found at the cotyledon, one true leaf, two true leaf, and three true leaf stages in Blackville, SC, 2015-2017 averaged for all samples.

Year	Fixed effect	Cotyledon		One True Leaf		Two True Leaves		Three True Leaves	
		DDF	F	DDF	F	DDF	F	DDF	F
2015	Planting Date	8,	5.8428 ^a	8,	11.5295 ^a	7,	5.0782 ^b	7, 42.43	7.7267 ^a
		58.18		58.25		52.14			
	Treatment	1, 58.2	8.5681 ^c	1,	0.6408NS	1,	0.0285NS	1, 42.24	1.6938NS
	Planting Date*Treatment	8,	2.5915 ^d	8,	0.9427NS	7,	0.8215NS	7, 42.23	0.3585NS
		58.18		58.25		51.14			
2016	Planting Date	7, 25.1	5.51 ^b	6,	17.2708 ^a	8, 16.7	5.77 ^c	6, 9.58	1.51NS
				19.03					
	Treatment	1, 29.3	16.69 ^b	1,	5.1153 ^d	1, 13.4	0.01NS	1, 6.73	0.00NS
	Planting Date*Treatment	6, 29.4	2.45 ^d	6,	0.8288NS	6, 13.4	0.46NS	5, 6.69	0.26NS
				26.52					
2017	Planting Date	9, 29.6	3.47 ^c	7, 73.1	11.55 ^a	9, 21.9	12.26 ^a	7, 17.7	9.40 ^a
		1, 74.7	2.32NS	1, 74.5	2.92NS	1, 65.7	0.05NS	1, 38.4	3.21NS
	Planting Date*Treatment	7, 74.7	1.07NS	7, 72.7	0.81NS	9, 61.7	0.30NS	7, 37.7	0.86NS
	Variety	1, 74.7	0.01NS	1, 73.1	2.13NS	1, 75.8	0.01NS	1, 44.5	3.60NS
	Planting Date*Variety	7, 74.7	0.32NS	7, 73.3	1.27NS	9, 69.9	1.96NS	6, 40.4	2.47 ^d
	Treatment*Variety	1, 74.7	0.11NS	1, 74	0.19NS	1, 62.9	2.03NS	1, 42.2	0.06NS
	Planting Date*Treatment*Variety	7, 74.7	0.41NS	5, 72.6	0.87NS	7, 60.3	0.50NS	6, 39.6	0.15NS

NS, not significant F, F Statistic DDF, degrees of freedom for numerator and denominator.

^a $P < 0.0001$

^b $P < 0.001$.

^c $P < 0.01$.

^d $P < 0.05$.

Table 1.3. ANOVA statistics for immature thrips found at the cotyledon, one true leaf, two true leaf, and three true leaf stages in Blackville, SC, 2015-2017

Year	Fixed effect	Cotyledon		One True Leaf		Two True Leaves		Three True Leaves	
		DDF	F	DDF	F	DDF	F	DDF	F
2015	Planting Date	8, 28.8	14.56 ^a	8, 28.4	4.44 ^b	7, 31.51	8.98 ^a	7, 20.1	26.32 ^a
	Treatment	1, 3.77	43.362 ^c	1, 3.16	14.02 ^b	1, 46.85	0.8NS	1, 2.37	3.17NS
	Planting Date*Treatment	8, 37.2	4.04 ^c	8, 39.9	0.94NS	7, 46.8	0.96NS	7, 19.8	0.8199NS
2016	Planting Date	7, 48	0.83NS	6, 19.1	2.60NS	8, 17.4	6.98 ^b	6, 17.7	4.87 ^c
	Treatment	1, 48	4.23 ^d	1, 21.7	10.54 ^c	1, 14.1	29.64 ^a	1, 17.1	0.12NS
	Planting Date*Treatment	6, 48	0.79NS	6, 20.4	2.08NS	6, 14.2	6.19 ^c	5, 17	0.17NS
2017	Planting Date	9, 32	4.15 ^c	7, 75	53.25 ^a	9, 23.1	5.85 ^b	7, 17.8	3.14 ^d
	Treatment	1, 75.2	4.70 ^d	1, 75	14.30 ^b	1, 74.3	16.97 ^a	1, 40.1	19.59 ^a
	Planting Date*Treatment	7, 75.2	3.25 ^c	7, 75	7.12 ^a	9, 70.7	1.38NS	7, 39.4	1.38NS
	Variety	1, 75.2	0.05NS	1, 75	0.08NS	1, 82.8	3.11NS	1, 46.2	1.65NS
	Planting Date*Variety	7, 75.2	0.89NS	7, 75	1.42NS	9, 78	1.43NS	6, 42.5	2.06NS
	Treatment*Variety	1, 75.4	1.22NS	1, 75	5.36 ^d	1, 73.5	3.25NS	1, 45.1	0.56NS
	Planting Date*Treatment*Variety	7, 75.3	0.62NS	5, 75	1.25NS	70.6	1.89NS	6, 41.9	0.54NS

NS, not significant F, F Statistic DDF, degrees of freedom for numerator and denominator.

^a $P < 0.0001$

^b $P < 0.001$.

^c $P < 0.01$.

^d $P < 0.05$.

Table 1.4. ANOVA statistics for thrips-days, injury, biomass, and yield in cotton trials in Blackville, SC, 2015-2017

Year	Fixed effect	Thrips-days		Injury		Biomass		Yield	
		DDF	F	DDF	F	DDF	F	DDF	F
2015	Planting Date	9, 27	12.36 ^a	9, 29.57	33.1708 ^a	9, 27	4.1614 ^b	9, 27	16.7374 ^a
	Treatment	1, 3	24.1819 ^d	1, 3.049	47.0047 ^c	1, 3	1.7741NS	1, 3	2.7904NS
	Planting Date*Treatment	9, 27	1.2856NS	9, 247.6	0.6113N	9, 27	1.4964NS	9, 27	2.7315 ^d
2016	Planting Date	9, 27.27	10.429 ^a	9, 16.02	119.9665	9, 27.18	21.9982 ^a	9, 27.06	5.4631 ^b
	Treatment	1, 3.016	37.0301 ^c	1, 2.868	21.7871 ^d	1, 3.147	1.4985NS	1, 2.569	0.0092NS
	Planting Date*Treatment	9, 27.12	3.5446 ^c	9, 335.6	1.3949N	9, 26.69	1.15NS	9, 25.48	3.805 ^c
2017	Planting Date	9, 27	21.7368 ^a	9, 26.73	14.9162 ^a	9, 27	77.1309 ^a	9, 27	10.8562 ^a
	Treatment	1, 3	17.5684 ^d	1, 3.162	37.36631 ^a	1, 3	1.8468NS	1, 3	0NS
	Planting Date*Treatment	9, 84	1.6020NS	9, 432	1.9113N	9, 84	0.9371NS	9, 84	0.8140NS
	Variety	1, 3	1.8157NS	1, 3.042	18.6469 ^d	1, 3	1.9667NS	1, 3	3.7497NS
	Planting Date*Variety	9, 84	0.7987NS	9, 432	1.9593 ^d	9, 84	0.9778NS	9, 84	2.9743 ^c
	Treatment*Variety	1, 84	0.7261NS	1, 432.1	2.2041N	1, 84	1.1463NS	1, 84	0.0135NS
Planting Date*Variety	9, 84	0.1937NS	9, 432	0.5921N	9, 84	1.4363NS	9, 84	1.4575NS	
Date*Treatment*Variety				S					

NS, not significant. F, F Statistic DDF, degrees of freedom for numerator and denominator.

^a $P < 0.0001$

^b $P < 0.001$.

^c $P < 0.01$.

^d $P < 0.05$.

CHAPTER THREE

EFFECTS OF VARIETAL SUSCEPTIBILITY ON DENSITY OF AND INJURY FROM THRIPS (THYSANOPTERA: THIRIPIDAE) IN COTTON

Introduction

Thrips (Thysanoptera: Thripidae) are consistent insect pests of cotton, *Gossypium hirsutum* L., in the United States (Cook et al. 2011). When thrips infest cotton, they feed on the epidermal and mesophyll cells of host plants (Wardle and Simpson 1927, Chisholm and Lewis 1984). Slower maturation and yield loss is common for cotton crops infested with thrips (Wilson 1982, Sandras and Wilson 1998). Severe infestation of thrips in cotton can result in the death of the apical meristem of the cotton plant and, during cool conditions, can lead to yield loss of up to 50% (Cook et al. 2011). To prevent yield loss, treatments of systemic insecticides (thiamethoxam, imidacloprid, and acephate) applied on the seed before planting or as granular materials (phorate or aldicarb) or liquid sprays (imidacloprid or acephate) in the furrow at planting are commonly used to control infestations of thrips in seedling cotton in the United States (Cook et al. 2011). While these treatments options have been effective in the past, recent research and supply of chemicals has raised questions as to the efficacy of chemical control options alone for successful control of thrips in cotton.

Supply of aldicarb, an effective insecticide for control of thrips, is low, and widespread resistance of the main pest species, *Frankliniella fusca* Hinds, to the neonicotinoid insecticides thiamethoxam and imidacloprid has developed in the United States (Huseth et al. 2016). As current options for chemical control of thrips are

becoming ineffective or limited in availability, alternative control strategies are needed to effectively manage thrips in seedling cotton. Because of the reduced supply and effectiveness of insecticides for control of thrips in cotton, use of host plant resistance (HPR) as a supplementary control tactic would be timely and preferred, if HPR could be identified in the crop. Host plant resistance can take the form of antibiosis, antixenosis, or tolerance. Antibiosis resistance affects the biology of the insect so that pest abundance and damage is reduced, and it results in increased mortality or reduced longevity and reproduction of the insect. Antixenosis also affects the behavior of the insect but results in non-preference of the insect for resistant plants compared with susceptible plants. Tolerance is resistance where the response to the interaction comes from the plant instead of the insect. Tolerant plant resistance results in a plant being able to recover or withstand more damage from an insect pest compared with a non-tolerant plant. All three forms of host-plant resistance can be found in cotton as the crop interacts with thrips.

Variability in densities of and injury from thrips has been documented among different varieties of cotton (Ramey 1962, Hawkins et al. 1966, Quisenberry and Rummel 1979, Zareh 1985, Leigh 1995, Arif et al. 2004, Miyazaki et al. 2017). Mechanisms for putative HPR traits include leaf morphology and constitutive chemicals that deter colonization or injury by thrips. Some morphological characteristics of cotton associated with resistance to thrips include pilosity (hairiness) (Ramey 1962, Quisenberry and Rummel 1979, Khan et al. 2014) or glabrousness (smoothness) of leaves (Zareh 1985, Leigh 1995), which are both reported to reduce injury associated with excessive densities of thrips. Thicker lower leaf epidermis and overall leaf thickness are also correlated with

reduced susceptibility to thrips (Arif et al. 2004). Cotton varieties with allelochemical components, such as higher levels of gossypol or tannins, have been observed to have a negative relationship with population development of thrips (Bourland and Benson 2002, Arif et al. 2006, Balakrishnan 2006, Khan et al. 2014). Because studies testing HPR traits for thrips in cotton have used non-isogenic lines, it has been difficult to measure the impact of selected traits, as results are often confounded by two or more traits concurrently contributing to HPR of cotton to thrips (Miyazaki et al. 2017). However, despite that complexity, results from previous studies on HPR of cotton to thrips indicated that morphological traits alone do not explain leaf damage scores in some cultivars of cotton (Miyazaki et al. 2017). While chemical composition of a cotton plant does determine its susceptibility to thrips, it does not permit identification of cotton varieties with potential HPR qualities without extensive laboratory and field testing. A study found that seed size was positively correlated with vigor of seedling cotton in the field (Snider et al. 2014). Cotton plants with higher dry weights are thought to be able to recover from thrips damage more readily than cotton plants with smaller dry weights.

Because of differences among varieties of cotton in their susceptibility and tolerance to thrips and the possibility of control failures from chemical management methods, the goal of this study was to evaluate a range of commercial cotton varieties for resistance to thrips in trials across the southeastern United States and to determine if the seed size and weight of the varieties has an effect on the ability of the variety to tolerate feeding injury from thrips.

Materials and methods

Locations and Design of Field Experiments

Field trials were conducted during 2016 and 2017 in five southern states (Virginia, North Carolina, South Carolina, Georgia, and Alabama) in the United States. Plots in each study were four or eight rows wide and 12.2 meters long (40 feet) and 3.85 (four rows) or 7.7 (eight rows) meters (26.67 feet) wide. Row spacing was 96.5 centimeters (38 inches), with three seeds planted per 30.5 centimeters (1 foot), and four replications. In 2016, data from each location were combined and analyzed as a split-plot design, with location as the main plot effect and variety of cotton as the sub-plot effect. In 2017, a split-split-plot design, with insecticide treatment as an additional split-split-plot effect was used (Table 2.1.). In each year and location, the same twelve commercially available varieties were included: which were PHY 312 WRF, PHY 333 WRF, PHY 444 WRF, and PHY 499 WRF (Dow AgroSciences, Indianapolis, IN); DP 1410 B2RF, DP 1518 B2XF, DP 1538 B2XF, and DP 1646 B2XF (Monsanto Company, St. Louis, MO); ST 4747 GLB2, ST 4946 GLB2, ST 6182 GLT, and FM 1900 GLT (Bayer CropScience, Research Triangle Park, NC). All seed in both years were treated with a fungicide consistent with commercial practice. In 2017, all treated plots at the Virginia, North Carolina, and Alabama locations received a broadcast foliar spray of acephate (Orthene 97, Amvac Chemical, Newport Beach, CA) at 0.42 kg AI/ha consistent with commercial practices in that state for managing thrips in seedling cotton. In the same year, all treated plots in South Carolina and Georgia received an at-plant treatment of phorate applied as an in-furrow granular material at 5.6 kg AI/ha (Thimet, Amvac Chemical, Newport Beach, CA). For seed measurements, two hundred seed from each variety were removed

randomly from their bag to determine the length, width, and weight of each seed. The length and width of each seed were measured in millimeters, and the weight of each seed was measured in milligrams. The volume of each seed was measured in (mm^3), and the density of each seed was measured in (g/mm^3).

Table 2.1. Year, locations, planting date, and cotton variety for trials measuring the susceptibility of cotton to thrips in Virginia, North Carolina, South Carolina, Georgia, and Alabama.

Year	Location	Planting Date	Insecticide	Variety
2016	Suffolk, Virginia (VA)	18 May	Untreated Only	
2016	Plymouth, North Carolina (NC)	5 May	Untreated Only	
2016	Blackville, South Carolina (SC)	4 May	Untreated Only	
2016	Tifton, Georgia (GA 1)	6 May	Untreated Only	PHY 312 WRF, PHY 333 WRF, PHY 444 WRF, PHY 499 WRF
2016	Tifton, Georgia (GA 2)	25 April	None	
2016	Prattville, Alabama (AL 1)	25 April	None	DP 1410 B2RF, DP 1518 B2XF, DP 1538 B2XF, DP 1646 B2XF,
2016	Belle Mina, Alabama (AL 2)	16 May	None	
2017	Suffolk, Virginia (VA)	4 May	Acephate @ .42 kg/ha foliar spray	ST 4747 GLB2, ST 4946 GLB2, ST 6182 GLT, FM 1900 GLT
2017	Plymouth, North Carolina (NC)	9 May	Acephate @ .42 kg/ha foliar spray	
2017	Blackville, South Carolina (SC)	27 April	Phorate @ 5.6 kg/ha In-furrow spray	
2017	Prattville, Alabama (AL)	14 April	Acephate @ .42 kg/ha foliar spray	
2017	Tifton, Georgia (GA)	20 April	Phorate @ 5.6 kg/ha In-furrow spray	

Data Collection

Density of thrips were determined for 4-5 consecutive weeks after the emergence of cotton seedlings. Thrips densities were measured using a destructive sampling technique where five or ten randomly selected plants were removed from each plot, with half pulled from row one and half pulled from row four when four-row plots were used, or half pulled from row two and half from row seven when eight-row plots were used. In the case where only five plants total were sampled from a plot, three plants were taken from its respective row and two were taken from the other respective row. After each plant was removed from the ground, it was immersed quickly and individually into a 1-liter jar of 50% isopropyl alcohol (before the next plant was removed) in the field. In the laboratory, jar contents (alcohol and thrips) from a single plot were poured onto #8 filter paper (Fisher Scientific, Waltham, MA) with a fast flow rate and coarse porosity, and Buchner funnels attached to an electric pump operating at a range of 0.7 to 3.4 bars were utilized in modified filtration procedures (Burriss et al. 1990) to accelerate the process of filtration. After filtration, numbers of adult and immature thrips on each filter paper were counted using dissecting microscopes.

Thrips injury ratings (Hawkins et al. 1966) were estimated visually using a modified 0-5 scale, where '5' was the most severe injury, and '0' represented no indication of feeding injury from thrips, with a single rating given for an entire plot. Heights from five or ten plants randomly selecting from the center two or four rows of each plot were measured. Plant heights were measured from the soil to the terminal growing point. Dry weight biomass was measured at one true leaf, four true leaves, and forty-two days after planting by randomly excising five plants at ground level from the

center two or four rows of each plot. Plants were then placed into drying ovens at 71°C for 48 hours before being weighed. Yields of seed cotton were determined from the middle two or four rows of each plot with a mechanical plot picker.

Data Analyses

In 2016, thrips densities, plant dry weights, and visual injury ratings were analyzed using a two-way analysis of variance as a split-plot design with variety, location (Virginia, North Carolina, South Carolina, Georgia, or Alabama), and their interaction as fixed effects. Replication was nested within location, and its interaction with variety modeled as random effects (Littell et al. 2006); PROC MIXED; (SAS Institute 2015). Means were separated using Tukey's HSD (Tukey 1953). Degrees of freedom were adjusted using the Kenward-Roger method (Kenward and Roger 1997). In cases where a location effect interacted with the variety effect, the SLICE (SAS Institute 2015) statement was used to determine differences among varieties at each location.

In 2017, thrips densities, injury ratings, dry weights, and seed cotton yields were analyzed as a three-way analysis of variance in a split-split-plot design with variety, location of experiment (Virginia, North Carolina, South Carolina, Georgia, and Alabama), insecticide treatment, and their interactions as fixed effects. Replication nested within location and its interaction with treatment were used as random effects (Littell et al. 2006, SAS Institute. 2015). Means were separated using Tukey's HSD (Tukey 1953). In cases where a location effect interacted with variety or treatment, the SLICE statement was used to determine differences among varieties at each location.

Data from field observations were compared with thrips densities and visual injury ratings using PROC CORR (SAS Institute 2015) to examine relationships between the density of adult and immature thrips and the dry weight and height of the plants. PROC CORR was also used to examine the relationship between visual injury observed in the field and dry weight and height of the plants. Seed volume was calculated by multiplying the seed length of each seed by the width of each seed.

Results

Adult Thrips

The effect of variety and the interaction with location did not have a significant effect on the density of adult thrips in 2016 (Table 2.2). The effect of location was significant in 2016 (Table 2.2), with the first Alabama location (AL 1) having the highest numbers of adults at 4.7 +/- 0.2. North Carolina had 3.8 +/- 0.2 adults, and the second Georgia (GA 2) location had 2.8 +/- 0.2 adults. The Virginia, Georgia, (GA 1), and South Carolina locations had the lowest number of adult thrips with 1.1 +/- 0.2, 0.8 +/- 0.2, and 0.7 +/- 0.2, respectively.

The density of adult thrips varied with location but not with variety in 2017 (Table 2.2, Fig 2.1).

2017

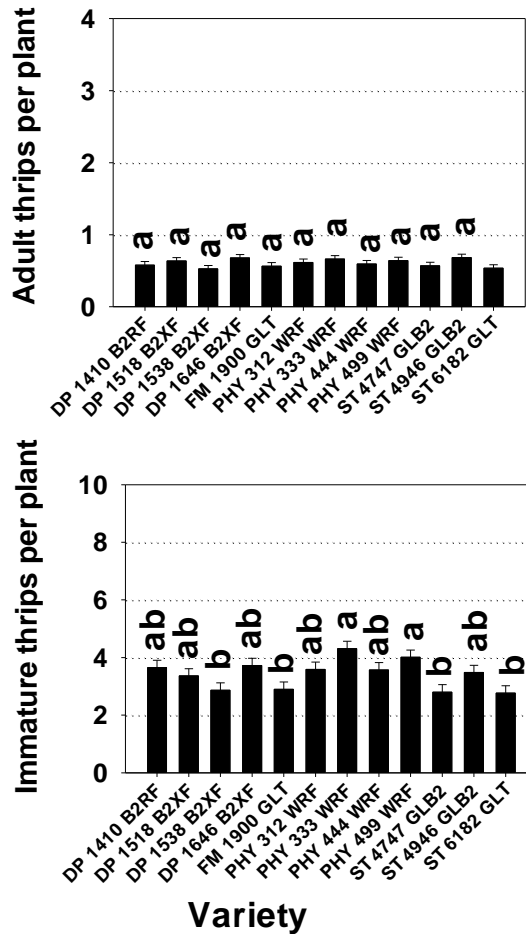


Figure 2.1. Impact of varietal susceptibility on thrips adult and immature density in cotton averaged across five locations in Virginia, North Carolina, South Carolina, Georgia, and Alabama in 2017. Bars with same letters are not significantly different (Tukey 1953).

The Georgia location had the highest mean density of adult thrips (11.2 +/- 0.62 adults per 10 plants) across sampling dates (Table 2.3). North Carolina and South Carolina had similar mean densities of adult thrips (8.1 +/- 0.62 and 7.9 +/- 0.62 adults per 10 plants, respectively), both of which were significantly more than Virginia and Alabama, but less than the Georgia location. The Virginia and Alabama locations had 4- and 28-fold fewer

adult thrips, respectively, than Georgia. The interaction between variety and location was significant in 2017 (Table 2.2). Using the SLICE option of PROC MIXED, the effect of variety was significant at the Georgia location (Table 2.3), where the highest mean density of adult thrips was 15.6 adults per 10 plants in PHY 333 WRF, and the lowest mean density of adult thrips was 7.7 adults per 10 plants in FM 1900 GLT, a 2-fold reduction (Figure 2.2). Significant differences also occurred at the North Carolina location (Table 2.3), where ST 4946 GLB2 had the highest density of adult thrips at 11.1 adult thrips per 10 plants, and PHY 333 WRF had the lowest density at 5 adult thrips per 10 plants, a 2.2-fold reduction (Figure 2.2). At the South Carolina location, the highest mean density of adult thrips was 10.4 adults per 10 plants in ST 4946 GLB2, and the lowest mean density of adult thrips

2017

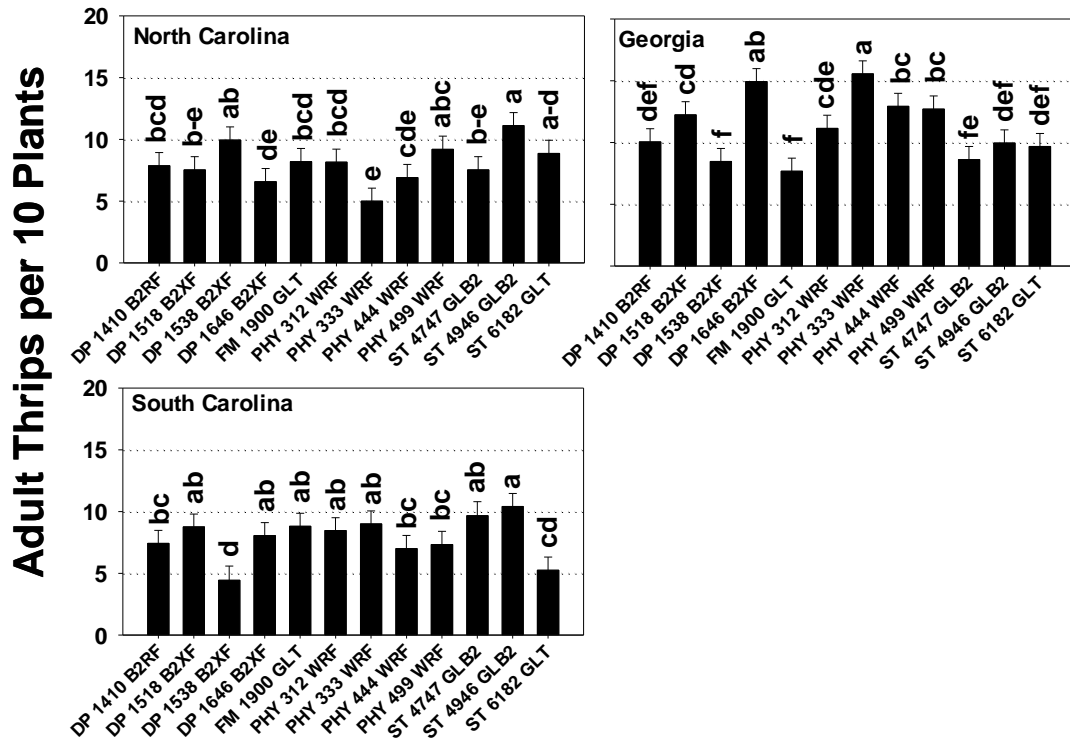


Figure 2.2. Impact of varietal susceptibility on adult thrips densities in cotton using SLICE effect by location in 2017. Bars with same letters are not significantly different (Tukey 1953).

was 4.3 adults per 10 plants in DP 1538 B2XF, 2.4-fold reduction (Figure 2.2).

Averaged across all locations and varieties in 2017, plots that received an insecticide application had a mean density of 5 adult thrips per 10 plants, while plots that were left untreated with insecticide had a mean density of 7.2 adult thrips per 10 plants, a 1.4-fold reduction. The interaction between location and insecticide, where the North Carolina site was the only site to observe a statistical reduction of adult thrips with insecticide use, saw plots that received a foliar application of acephate at 0.42 kg/ha have a (3.9-fold) reduction in adult thrips.

Immature Thrips

The effects of variety and the interaction with location were not significant for immature thrips in 2016 (Table 2.2). Immature thrips were most abundant on the earliest planted Georgia location (GA 2) and the Virginia location with 13 ± 0.5 and 9 ± 0.5 immature thrips, respectively (Table 2.3). The Georgia (GA 2) and Virginia locations both had significantly more thrips than the North Carolina, Alabama, and South Carolina locations which had 2.2 ± 0.5 , 0.6 ± 0.4 , and 0.5 ± 0.5 thrips, respectively. The effect of variety and its interaction with location were not significant for immature thrips in 2016 (Table 2.2).

2017

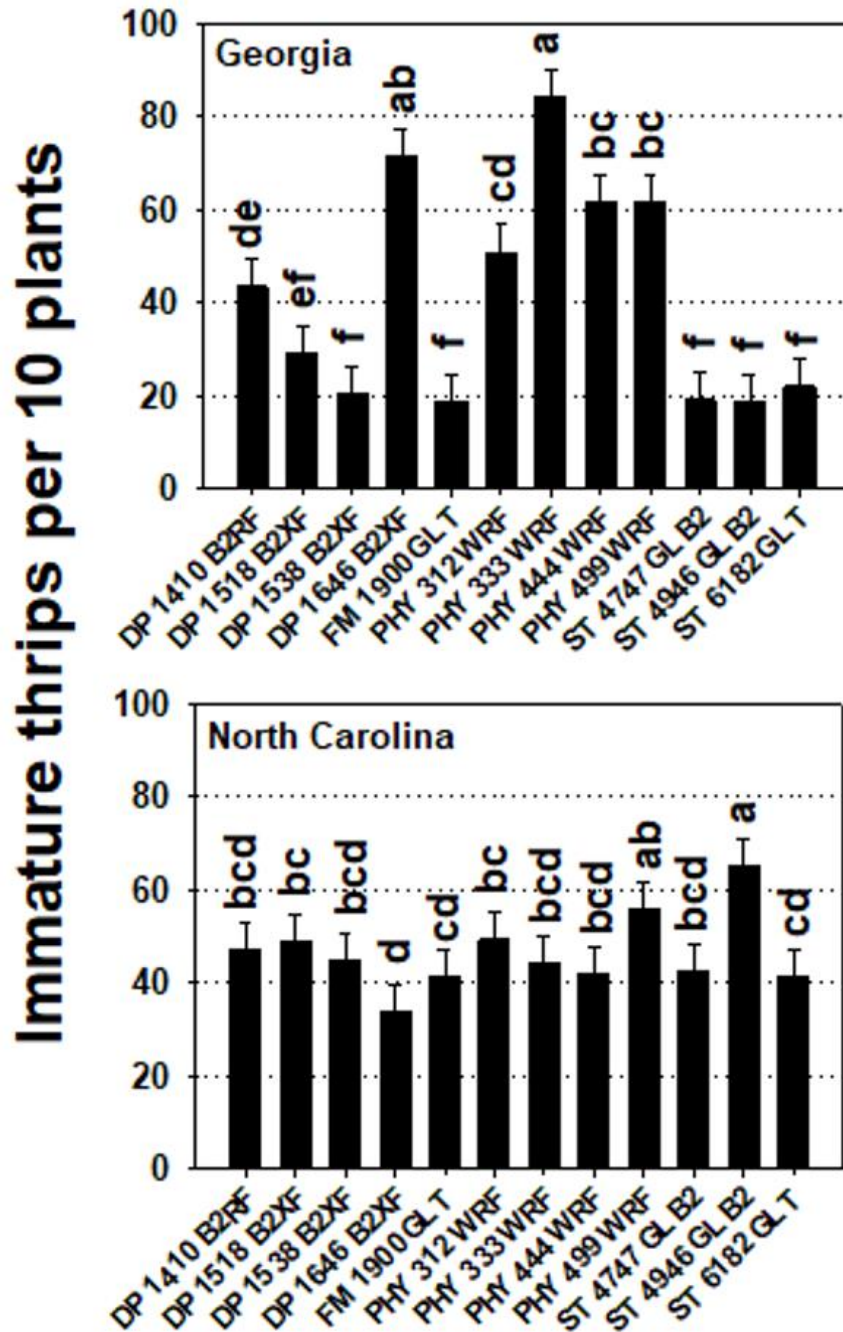


Figure 2.3 – Impact of varietal susceptibility on immature thrips densities in cotton using SLICE effect by location in 2017. Bar with same letters are not significantly different (Tukey 1953)

Variety had a significant effect on the density of immature thrips in 2017, but not in 2016 (Table 2.2). Averaged across all locations, PHY 333 WRF had 4.3 immature thrips, while ST 6182 GLT had 2.77 immature thrips, a 1.5-fold reduction (Figure 2.1). In 2017, South Carolina, which had 9.9 +/- 2.6 immature thrips per 10 plants, which was significantly less than North Carolina, Georgia, Alabama, and Virginia which had 46.4 +/- 2.6 , 41.8 +/- 2.6 , 37.0 +/- 2.6, and 35.7 +/- 2.6 immature thrips per 10 plants, respectively. The interaction between variety and location was significant in 2017 (Table 2.2). In Georgia, PHY 333 WRF averaged 84.5 immature thrips per 10 plants, and ST 4946 GLB2 had 18.7 immature thrips, a 4.5-fold reduction (Figure 2.3).

In North Carolina, ST 4946 GLB2 averaged 65.3 immature thrips per 10 plants, and DP 1646 B2XF averaged 1.9-fold less, with 34.0 immature thrips per 10 plants (Figure 2.3). No differences in numbers of immature thrips were detected among varieties in Alabama, South Carolina, or Virginia in 2017 (Figure 2.3). The interaction between location and treatment was significant in 2017 (Table 2.2).

Thrips Damage Ratings

When the injury ratings for all locations were averaged together by variety in 2016 and 2017 significant differences occurred (Table 2.2, Figure 2.4).

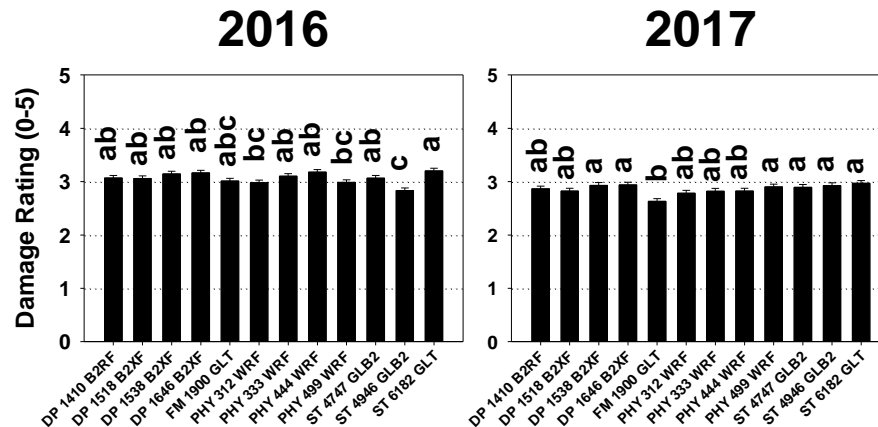


Figure 2.4. Impact of varietal susceptibility on visual injury ratings in cotton averaged across seven locations in Virginia, North Carolina, South Carolina, Georgia, and Alabama in 2016 and across five locations in Virginia, North Carolina, South Carolina, Georgia, and Alabama in 2017. Bars with same letters are not significantly different (Tukey 1953).

In 2016 significant differences in injury among varieties of cotton occurred at the Alabama 1, Alabama 2, and Georgia 1, and North Carolina locations (Table 2.3, Figure 2.5). ST 4946 GLB2, FM 1900 GLT, were generally among the varieties with the lowest injury ratings (Figure 2.5). The injury rating of ST 4946 GLB2 was 2.9 at the Alabama 1 location, 3.4 at the Alabama 2 location, 2.9 at the Georgia 1 location, and 2.6 at the North Carolina location (Figure 2.5) The injury rating of FM 1900 GLT was 2.9 at the Alabama 1 location, 2.8 at the Alabama 2 location, 3.3 at the Georgia 2 location, and 2.8 at the North Carolina location (Figure 2.5) The largest injury at the Alabama 1 location was 3.4, 3.4 at the Alabama 2 location, 4 at the Georgia 1 location, and 3.6 at the North Carolina location.

2016

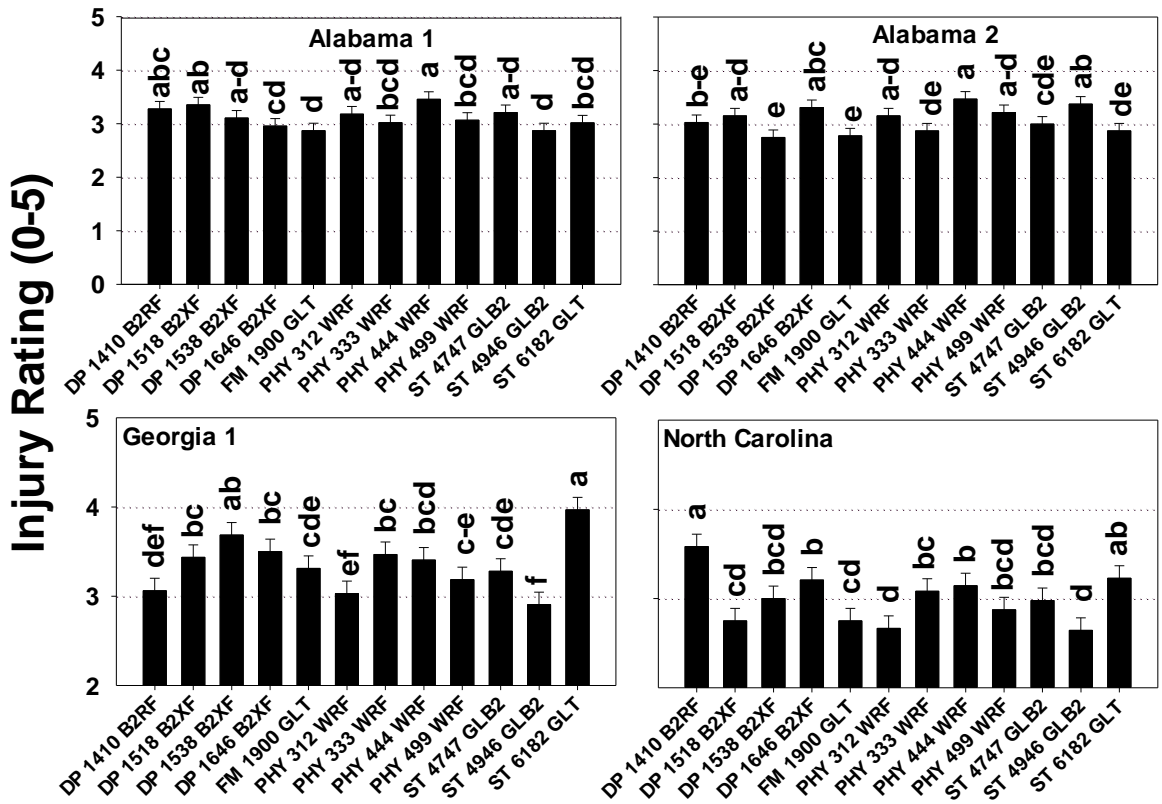


Figure 2.5. Impact of varietal susceptibility on visual injury ratings in cotton using SLICE effect by location in 2016. Bars with same letters are not significantly different (Tukey 1953).

2017

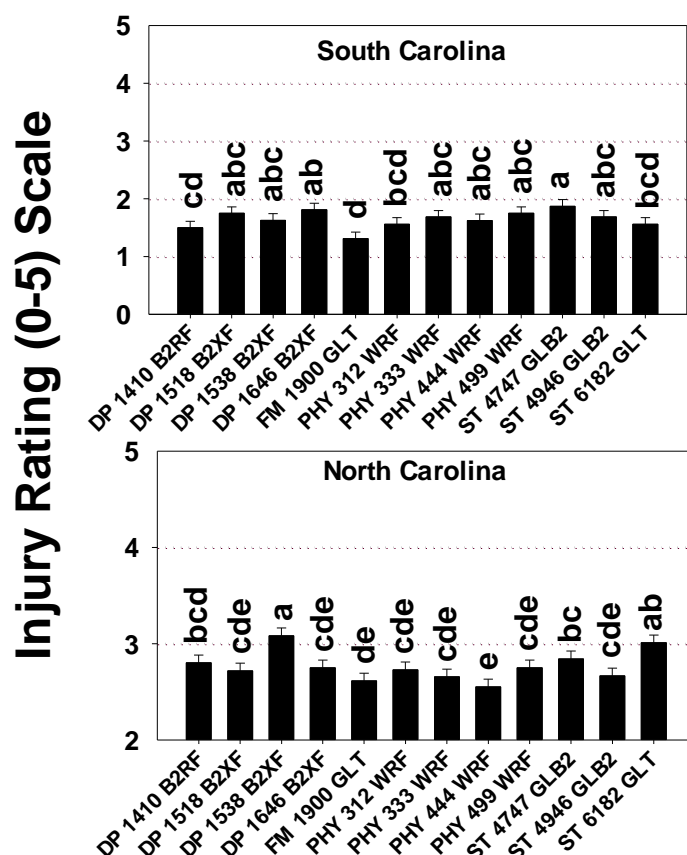


Figure 2.6. Impact of varietal susceptibility on visual injury ratings in cotton using SLICE effect by location in 2017. Bars with same letters are not significantly different (Tukey 1953)

In 2017, ST 4946 GLB2 was not consistently among the least injured varieties of cotton (Figure 2.6). ST 4946 GLB2 had an injury rating of 1.7 at the South Carolina location while the most injured variety had an injury rating of 1.9 (Figure 2.6).

At the North Carolina location ST 4946 GLB2 had an injury rating of 2.7 and the most injured variety had an injury rating of 2.85 (Figure 2.6). FM 1900 GL was among the least injured varieties at the South Carolina location in 2017 with an injury rating of 1.3, while the highest injury at the South Carolina location was 1.9 (Figure 2.6). At the North Carolina

location, FM 1900 GLL had an injury rating of 2.6, while the highest injury was 3.1 (Figure 2.6).

Yield

Averaged across locations, the largest differences among varieties in yield were between PHY 444 WRF (3268 kg/ha) and DP 1538 B2XF (2839 kg/ha). In 2017, the effect of the interaction between variety and location was significant (Table 2.3). In Alabama, the largest difference in yield was between PHY 444 WRF (3185 kg/ha) and ST 4946 (2329 kg/ha), a 1.4-fold reduction (Figure 2.7).

The effect of variety was not significant for yield in Georgia. In North Carolina, the greatest difference occurred between DP 1410 B2RF (2891 kg/ha) and both FM 1900 GLT (2233 kg/ha) and ST 4946 GLB2 (2238 kg/ha) (Figure 2.7). DP 1410 B2RF yielded 1.3-fold higher than FM 1900 GLT at the North Carolina location. At the South Carolina location, ST 4946 GLB2 yielded 3771, which was not significantly different than PHY 444 WRF. However, ST 4946 GLB2, which yielded 3771, yielded higher than DP 1410

2017

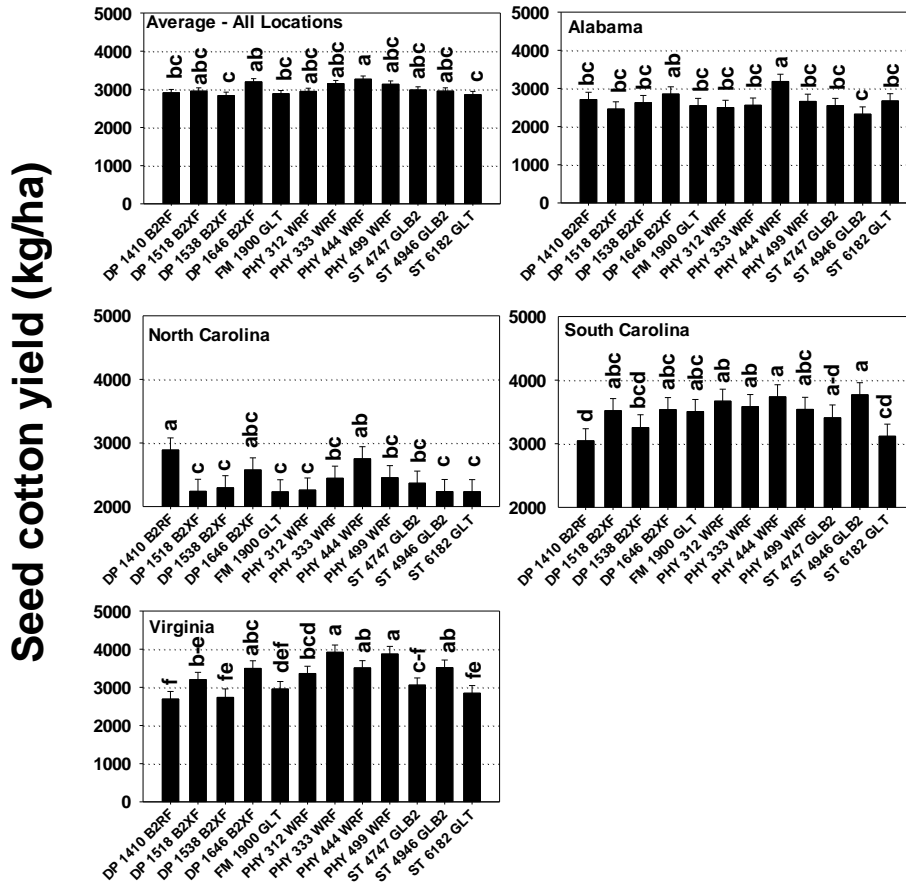


Figure 2.7. Impact of varietal susceptibility on seed cotton yield (kg/ha) averaged across five locations (Average and using SLICE effect by location in 2017. Bars with same letters are not significantly different (Tukey 1953).

B2RF, which only yielded 3048, a 1.23-fold reduction in yield (Figure 2.7). At the Virginia location, PHY 333 WRF and PHY 499 WRF did not differ significantly in their yields, which were 3920 and 3876 respectively (Figure 2.7). PHY 333 WRF and PHY 499 WRF did not yield significantly more than ST 4946 GLB2, which yielded 3517. PHY 333 WRF, PHY 499 WRF, and ST 4946 GLB2, all yielded 1.3-fold higher than FM 1900 GLT, which only yielded 2955. The largest difference in yield at the Virginia location occurred where PHY 333 WRF yielded 3920 and DP 1410 B2RF yielded 2690,

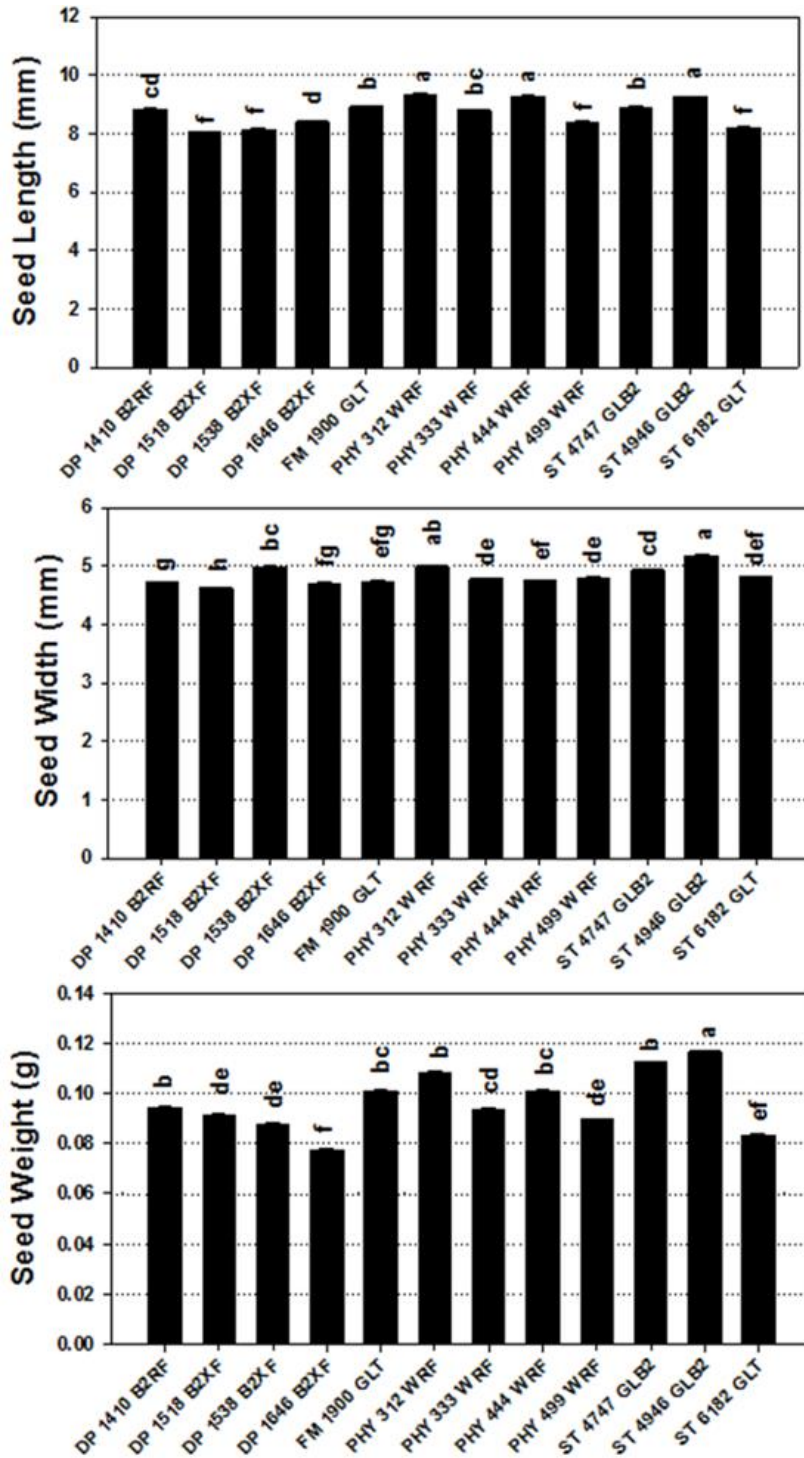


Figure 2.8. Impact of variety of cotton on seed length (mm), seed width (mm), and seed weight. Bars with the same letters are not significantly different (Tukey 1953).

a 1.5-fold reduction (Figure 2.7). The interaction between variety, location, and treatment was not significant in 2017 (Table 2.3).

Discussion

The results of this study indicated that several locations had varieties with significantly different numbers of immature thrips (Figure 2.1). Other authors have noted differences in thrips densities between different cotton varieties (Arif et al. 2006). Averaged across trials, FM 1900 GLT, ST 4747 GLB2, DP 1538 B2XF, and ST 6182 GLT had lower numbers of immature thrips compared with PHY 333 WRF and PHY 499 WRF in 2017 (Figure 2.1). Although statistical differences in the densities of adult thrips across varieties were detected in Georgia, North Carolina, and South Carolina in 2017, where densities exceeded 5 adults per plant (Figure 2.2), the exact cause of differences among varieties remains uncertain. Larval mortality of thrips can occur on plants that exhibit antibiosis (Frei et al. 2003), which is particularly effective in the case of thrips, as larval thrips are usually confined to the plant where oviposition occurs, at least until they pupate (Terry 1997). Larval thrips are an important indicator of the potential of a thrips infestation to cause damage. At the Georgia location, densities of immature (Figure 2.3) thrips differed significantly across varieties. In addition to differences in densities of adult and immature thrips, differences in visual injury ratings are known to exist between different varieties of cotton (Arif et al. 2006, Ballard 1951, Miyazaki et al. 2017).

Overall mean injury across locations was higher and more variable in 2016 than in 2017 (Figure 2.4), most likely from the relatively larger densities of thrips in 2016. When

injury ratings for ST 4946 GLB2 were averaged across locations in 2016, ST 4946 GLB2 had a lower injury rating than most other varieties included in the trial (Figure 2.4).

However, if considering each location separately, ST 4946 GLB2 was only among the lowest injury ratings at the Alabama 1, Georgia 1, and North Carolina locations. ST 4946 GLB2 was among the most injured varieties at the Alabama 2 location, and no differences among varieties were detected at the Virginia and South Carolina locations in 2016. In 2017, no differences in injury ratings were detected at the Virginia and Georgia locations (Figure 9), although treatments of insecticides significantly reduced injury at both locations (Figure 8). Differences in injury ratings among varieties were detected at the South Carolina and North Carolina locations in 2017 (Figure 9). FM 1900 GLT was among the varieties with the lowest injury at both the North Carolina and South Carolina locations. DP 1538 B2XF was among the highest injured varieties at the North Carolina and the South Carolina locations in 2017. While FM 1900 GLT was among the varieties with the lowest injury rating, it had significantly lower yield at the North Carolina location.

One characteristic that can be measured without the need for extensive field trials of different cotton varieties that could play a role in the susceptibility of a cotton variety to thrips is seed size and weight. ST 4946 GLB2, which generally had low injury ratings, was among the varieties of cotton with the largest and heaviest seed. However, other varieties such as FM 1900 GLT, which had an average seed size, were also among the lower spectrum of the thrips injury scale. This means that seed size alone was not the only factor to determine cotton injury from thrips. Ultimately, the exact reasons for the reduction in thrips injury for plots of cotton with larger seed width and volume are difficult to determine

from the results of this study. One possible explanation for the reduction in injury is more vigorous growth resulting from the larger seeds that gives large seeded cotton the ability to tolerate larger densities of thrips. More vigorously growing cotton is also larger in size and thus a smaller percentage of its weight is lost from thrips feeding when it is compared to a smaller plant and when both plants have the same thrips density feeding on them. However, dry weight observations in the field are not correlated with the same seed characteristics that are correlated with thrips injury. Another possibility is the ability of cotton with a larger seed to produce defensive compounds that reduce thrips densities, however no correlation between immature thrips densities were detected between any seed size or weight parameters in either year. Ultimately, the reasons for the correlation between seed size and thrips injury remain unknown because too many possibilities exist that could explain the differences in dry weight. Further investigation of seed size as a characteristic of cotton that lends itself to confer reduced susceptibility to thrips is warranted as selection of varieties of cotton with high seed quality and robust seed size and weight are correlated with lower thrips injury and could be an important management tool to consider when managing thrips in cotton.

While selection of varieties of cotton with reduced susceptibility could be an important part of an integrated pest management program, a promising option for the future includes a novel Bt event MON 88702 in cotton that expresses Cry151Aa2.834_16, with reported activity on thrips (Bachman et al. 2017). Although the toxin is effective in significantly reducing densities of and feeding injury from thrips, it will not be available for commercial use for a number of years. Until new methods of management for thrips

are available, sustainable production of cotton will need to rely on minimizing the use of insecticides by selecting varieties of cotton with reduced susceptibility to thrips. Characteristics that confer reduced susceptibility to thrips injury without compromising yield should be selected for in cotton for sustainable management of thrips in light of recent management challenges caused by reduced susceptibility of thrips to insecticides and loss of management options for thrips.

Table 2.2 ANOVA statistics for adult thrips, immature thrips, injury and yield for cotton trials in Virginia, North Carolina, South Carolina, Georgia, and Alabama 2016-2017.

Year	Fixed effect	Adult Thrips		Immature Thrips		Injury		Yield	
		DDF	F	DDF	F	DDF	F	DDF	F
2016	Variety	11, 340.5	0.9NS	11, 193.6	0.88NS	11, 227.2	3.07 ^b	N/A	N/A
	Location	5, 17.84	113.6 ^a	5, 17.5	20.46 ^a	6, 20.95	174 ^a	N/A	N/A
	Location*Variety	55, 295.3	0.96NS	55, 193.6	0.68NS	66, 227.2	2.34 ^a	N/A	N/A
2017	Variety	11, 328.1	1.67NS	11, 328.2	4.49 ^a	11, 261.8	3.27 ^b	11, 321.1	4.08 ^a
	Location	4, 14.97	48.39 ^a	4, 15.04	30.4 ^a	3, 11.62	430.28 ^a	4, 14.89	14.7 ^a
	Treatment	1, 15.04	19.97 ^b	1, 15.03	31.92 ^a	1, 12.03	332.96 ^a	1, 15.25	6.37 ^d
	Location*Variety	44, 328.1	3.16 ^a	44, 328.2	5.1 ^a	33, 261.8	1.86 ^c	44, 321	2.55 ^a
	Variety*Treatment	11, 328.1	0.59NS	11, 328.2	0.67NS	11, 261.8	1.27NS	11, 321.1	0.26NS
	Location*Treatment	4, 15.04	14.58 ^a	4, 15.03	7 ^c	3, 12.03	9.64 ^b	4, 15.21	2.03NS
	Variety*Location* Treatment	44, 328.1	0.74NS	44, 328.2	0.54NS	33, 261.8	1.3NS	44, 321	0.55NS

NS, not significant F, F Statistic DDF, degrees of freedom for numerator and denominator.

^a $P < 0.0001$

^b $P < 0.001$.

^c $P < 0.01$.

^d $P < 0.05$.

Table 2.3. ANOVA statistics for adult thrips, immature thrips, thrips injury, and seed cotton yield with SLICE effect by location 2016-2017.

Year	Location	Fixed Effect	Adult Thrips		Immature Thrips		Injury		Yield	
			DDF	F	DDF	F	DDF	F	DDF	F
2016	AL1	Variety	11, 637.5	1.82NS	11, 674.9	0.01NS	11, 227	2.02 ^d		
	AL2	Variety					11, 227	3.27 ^c		
	SC	Variety	11, 809.8	0.05NS	11, 826.7	0.01NS	11, 227	0.85NS		
	GA1	Variety	11, 809.8	0.20NS	11, 826.7	0.23NS	11, 227	5.10 ^a		
	GA2	Variety	11, 682.9	0.43NS	11, 691.8	0.83NS	11, 228.4	1.11NS		
	NC	Variety	11, 809.8	0.71NS	11, 826.7	0.10NS	11, 227	4.48 ^a		
	VA	Variety	11, 809.8	0.08NS	11, 826.7	0.56NS	11, 227	0.43NS		
2017	AL	Variety	11, 328	0.04NS	11, 328.1	0.73NS			11, 320.3	1.96 ^d
	GA	Variety	11, 328	7.59 ^a	11, 328.1	20.37 ^a	11, 669.9	1.42NS	11, 320.3	1.58NS
	NC	Variety	11, 328	3.04 ^b	11, 328.1	2.35 ^c	11, 63.4	4.17 ^b	11, 320.3	2.02 ^d
	SC	Variety	11, 328.3	3.31 ^b	11, 328.5	0.27NS	11, 262.8	1.91 ^d	11, 320.9	2.16 ^d
	VA	Variety	11, 328	0.28NS	11, 328.1	1.24NS	11, 63.4	0.63NS	11, 322.9	6.22 ^a

NS, not significant F, F Statistic DDF, degrees of freedom for numerator and denominator.

^a $P < 0.0001$

^b $P < 0.001$.

^c $P < 0.01$.

^d $P < 0.05$.

Table 2.4. Pearson correlation coefficients for dry weight and plant height correlated against adult thrips, immature thrips, and thrips injury ratings.

Year	Fixed effect	Adult Thrips			Immature Thrips			Thrips Injury Rating		
		n	r	P	n	r	P	n	r	P
2016	Dry Weight	371	-0.09NS	0.09	371	0.35 ^a	<0.0001	527	-.18 ^a	<0.0001
	Height	705	0.17 ^a	<.0001	705	-0.1 ^c	.01	816	0.03NS	0.42
2017	Dry Weight	1052	-0.13 ^a	<0.0001	1052	-0.24 ^a	<0.0001	670	-0.16 ^a	<0.0001
	Height	1532	-0.14 ^a	<0.0001	1532	-0.22 ^a	<0.0001	864	-0.17 ^a	<0.0001

n, number of observations r, Rho value P, P-value

Table 2.5. Average Seed Length (mm), Seed Width (mm), Seed Weight (g), Seed Volume (mm³), and Seed Density (g/mm³) by variety.

Variety	Seed Length		Seed Width		Seed Weight		Seed Volume		Seed Density	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
DP 1410 B2RF	8.85	0.02	4.71	0.012	0.09	.0005	41.68	0.2	0.00227	0.00001
DP 1518 B2XF	8.05	0.02	4.63	0.012	0.09	.0005	37.34	0.2	0.00247	0.00001
DP 1538 B2XF	8.15	0.02	4.99	0.012	0.09	.0005	40.62	0.2	0.00216	0.00001
DP 1646 B2XF	8.41	0.02	4.7	0.012	0.08	.0005	39.5	0.2	0.00196	0.00001
FM 1900 GLT	8.93	0.02	4.74	0.012	0.1	.0005	42.3	0.2	0.00239	0.00001
PHY 312 WRF	9.3	0.02	5	0.012	0.11	.0005	46.61	0.2	0.00232	0.00001
PHY 333 WRF	8.81	0.02	4.78	0.012	0.09	.0005	42.08	0.2	0.00223	0.00001
PHY 444 WRF	9.28	0.02	4.76	0.012	0.1	.0005	44.16	0.2	0.00228	0.00001
PHY 499 WRF	8.39	0.02	4.8	0.012	0.09	.0005	40.3	0.2	0.00222	0.00001
ST 4747 GLB2	8.91	0.02	4.93	0.012	0.11	.0005	43.97	0.2	0.00255	0.00001
ST 4946 GLB2	9.25	0.02	5.17	0.012	0.12	.0005	47.91	0.2	0.00244	0.00001
ST 6182 GLT	8.21	0.02	4.81	0.012	0.08	.0005	39.49	0.2	0.00211	0.00001

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