1318 Utilization of Resistance and Tolerance to Root-Knot Nematode in Cotton

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The southern root-knot nematode, *Meloidogyne incognita*, is the most damaging pathogen of cotton in the USA. Host-plant resistance to root-knot nematodes is an effective means of reducing crop losses and reducing nematode population levels in a field. Resistance to plant-parasitic nematodes refers to the suppressive effect of the plant on the nematode's ability to reproduce; tolerance describes the degree of damage caused by the nematode to the plant. Resistance to root-knot nematodes in cotton is correlated with tolerance, so crop loss decreases as the level of resistance increases. Cotton genotypes with the highest yield in the absence of nematode damage tend to have greater percentage losses when damaged by nematodes because nematodes prevent the plant from fully exploiting favorable growing conditions. Consequently, effective nematode management is increasingly important and beneficial in genotypes with the highest yield potentials. When either moderately resistant or highly-resistant cotton is grown, for one or more years, root galling and nematode population densities in the soil are significantly lower compared to a susceptible standard. Development of host-plant resistance to *M. incognita* in cotton using traditional breeding techniques has been difficult because it is very labor intensive and involves multiple resistance genes. Recent advances in identification of DNA markers for nematode resistance genes shows great promise, and should lead to the rapid development of resistant genotypes. Limited sources of resistance genes may increase selection pressure on nematode populations and lead to loss of efficacy of resistance genes.

Key words: *Gossypium hirsutum*, host-plant resistance, *Meloidogyne incognita*, southern root-knot nematode, tolerance.

Nematodes cause greater yield losses in cotton (*Gossypium hirsutum* L.) than any other pathogen, and the southern root-knot nematode (*Meloidogyne incognita* (Kofoid & White) Chitwood) causes more damage to cotton in the USA than any other nematode (Blasingame and Patel, 2005). Root-knot nematodes are distributed throughout the cotton-growing regions of the world. Their feeding causes root damage and extensive galling, resulting in reduced water and nutrient translocation in the cotton plant (Thomas and Kirkpatrick, 2001). Cotton yield losses worldwide due to this pest have been estimated to be 10.7% (Sasser and Freckman, 1987). In the USA alone, root-knot nematodes cause an estimated loss of 273 million pounds of lint annually (Blasingame and Patel, 2005). In addition to direct losses from nematode parasitism, infection by this nematode greatly increases the incidence and severity of Fusarium wilt caused by *Fusarium oxysporum f.* sp. *Vasinfectum* (Atk.) Snyd. & Hans., which causes an estimated loss of another 54.5 million pounds of lint annually in the USA (Blasingame and Patel, 2005). Although nematicides and crop rotation can be effective for managing this nematode, the development and use of resistant cultivars offers the best management tool for controlling root-knot nematodes.

Host-plant resistance to nematodes has several advantages for cotton growers over nematode management options such as nematicide application and crop rotation. Nematicides add a significant expense to crop production, and the effectiveness of nematicides can be reduced by adverse environmental conditions (Hague and Gowen, 1987; Lembright, 1990). For a crop rotation sequence to be acceptable, the alternate crop must maintain profitability and reduce nematode levels enough to increase yields in the following cotton crop. Nematode resistant cotton genotypes do not add to the cost of production, do not require calibration or additional effort to use, should not be affected by environmental conditions, are more consistently effective than nematicides, and will not reduce profitability.

Action thresholds are used to estimate the nematode population level at which reduced crop yield will justify the expense of nematicide application, but variability and inaccuracies in sampling and estimating nematode population levels, as well as the unpredictability of the actual level of crop loss to be sustained, reduce the accuracy of such thresholds. The use of host-plant resistance may eliminate concerns over inaccurate thresholds because there is no economic penalty for growing a resistant genotype when nematode population levels are below traditional threshold levels. However, seed companies may charge a premium for nematode-resistant cultivars, thereby creating an incentive to grow resistant cultivars only where nematode pressure warrants it.

RESISTANCE AND TOLERANCE TO NEMATODES

1Host-plant resistance to plant-parasitic nematodes is defined as the suppressive effect of the plant on the nematode's ability to reproduce (Cook and Evans, 1987). In contrast, tolerance describes the degree of damage, usually measured in terms of yield suppression, caused by a specific level of the nematode to the plant (Cook and Evans, 1987). Resistance and tolerance may be expressed simultaneously, or they can be inherited and expressed independently resulting in plants that are resistant but intolerant or tolerant but susceptible (Barker, 1993; Boerma and Hussey, 1992; Cook and Evans, 1987; Evans and Haydock, 1990). Plants that are tolerant but have no resistance will suffer less damage even though levels of parasitism are not reduced. Both host-plant resistance and tolerance could be useful for managing nematodes in crops (McSorley, 1998; Potter and Dale, 1994; Reese et al., 1988; Seinhorst, 1970; Young, 1998). Resistance in cotton to *Meloidogyne incognita* has been studied extensively 1(Cook et al., 1997; Ogallo et al., 1997; Robinson et al., 1999; Shepherd, 1974; Shepherd, 1983). In contrast, tolerance to *M. incognita* in cotton has received relatively little attention (Davis and May, 2003; Davis and May, 2005).

Plants highly resistant to nematodes are often tolerant to nematodes as well because they endure significantly less parasitism than susceptible plants when exposed to the same soil population densities of nematodes (Evans and Haydock, 1990). However, even highly resistant plants may be intolerant if the mechanism of resistance is a strong, localized hypersensitive response that causes root necrosis (Roberts, 1992), as is the case with sugar beets (*Beta vulgaris*) with resistance to *H. schachtii* derived from *B. procumbens* (McFarlane et al., 1982). Intolerant plants may appear to be resistant if nematode feeding reduces the amount of root tissue thereby reducing potential nematode feeding sites (Young, 1998). Because host-plant resistance can affect plant tolerance to nematodes, resistant plants should be evaluated for nematode tolerance (Roberts, 1992). In cotton, highly resistant germplasm lines (e.g., Auburn 623 RNR and M-120 RNR) appear to be very tolerant to root-knot nematode parasitism.

Davis and May (2003) studied tolerance in moderately resistant cotton germplasm lines. As the level of root-knot nematode resistance increased and fewer nematodes were able to complete their life cycle, the level of nematode tolerance increased (Fig. 1). They described the relationship between resistance and tolerance in cotton as analogous to a damage function relating nematode population density and damage. Zhou and Starr (2003) also reported that resistance to nematodes imparted tolerance to nematodes. The level of tolerance imparted by resistance will likely be proportional to the level of resistance, so that high levels of resistance will reduce yield losses in cotton greatly, but moderate levels of resistance will likely impart only moderate tolerance. However, any level of tolerance should be beneficial. The mechanism of tolerance in cotton is not known, but a genotype tolerant to one species might also be tolerant to other nematodes, though that has not been demonstrated.

Nematicide use may still be beneficial even when moderately resistant cotton genotypes are grown if nematode population levels are above the damage threshold (Koenning et al., 2001). For example, the yield of the moderately resistant cotton cultivar Stoneville LA 887 was increased by nematicide application in an *M. incognita*-infested field (Colyer et al., 1997). Some of the moderately resistant breeding lines studied by Davis and May (2003) had improved yields when a nematicide was used, but other lines with the same moderate level of resistance consistently showed no increase when treated with nematicides. Therefore, nematode tolerance in moderately resistant genotypes must be evaluated on a case-by-case basis. If significant tolerance can be incorporated into moderately resistant cultivars, the result should be reduced crop losses and improved profits for growers. However, even moderately resistant genotypes would be expected to have suppressed yields at very high nematode population densities or if Fusarium wilt is present. Use of resistant and tolerant varieties, especially if resistance is moderate, may require modification of existing action thresholds for the recommendation of nematicide application.

RELATIONSHIP OF YIELD POTENTIAL TO PERCENTAGE LOSS TO NEMATODES

"Yield potential" is a term that means "the yield of a cultivar when grown in environments to which it is adapted; with nutrients and water non-limiting; and with pests, diseases, weeds, lodging and other stresses effectively controlled" (Evans and Fischer, 1999). When cotton is parasitized by *M. incognita*, yields will be below the yield potential. A study designed to evaluate root-knot nematode tolerance in cotton led to the conclusion that percentage yield suppression caused by *M. incognita* increased as yield potential increased (Figure 2) (Davis and May, 2005). That is, genotypes with the highest yield in the absence of nematode damage tended to have greater percentage losses when damaged by nematodes. The relationship between yield potential and percentage yield suppression was significant even when the effect of nematode population density was considered, and the relationship (regression slopes and intercepts) was consistent during two years of field study.

A damage function that relates yield suppression to nematode population density is

$$y = \frac{yield_P - yield_{min}}{yield_{max} - yield_{min}}$$

where y = the relative yield (between 0.0 and 1.0) at nematode density P; $yield_P$ = yield at nematode density P; $yield_{min}$ = a minimum yield that will be achieved even at the highest nematode densities; and $yield_{max}$ = a maximum yield achieved in the absence of nematodes (Seinhorst, 1965). $Yield_{max}$ in Seinhorst's equation would be the crop's yield potential when other limiting factors are effectively minimized. For a specific nematode population density, the relative yield will decrease if the yield potential increases. This predicts that nematode parasitism will decrease yield by a greater percentage as yield potential increases, which was observation documented by Davis and May (2005). If both the absolute and percentage losses to nematodes increase when yield potential increases, then nematode management becomes increasingly important and beneficial.

Yield potential can be increased through breeding and selection for genotypes that allow the plants to be more responsive to inputs and exploit favorable growing conditions (Fasoula and Fasoula, 2002; Pala et al., 2004; Tokatlidis and Koutroubas, 2004). Although genotypes usually are evaluated under a range of conditions, cultivars often are selected based on outstanding performance in favorable environments (Calhoun et al., 1994). *Meloidogyne incognita* infection impairs root function and limits growth of the root system, which reduces a plant's ability to exploit favorable environments fully. If nematode parasitism inhibits exploitation of favorable growing conditions, then the percentage yield suppression would be greater for input-responsive genotypes (which have higher yield potentials) than for genotypes that were less capable of exploiting favorable conditions.

MULTI-SEASON EFFECTS

Nematode-resistant cultivars may be most valuable if they reduce nematode reproduction enough to affect the residual nematode population density in a field. Logically, highly resistant genotypes should suppress nematode levels more than moderately resistant genotypes. The benefits of crop rotations which include *Meloidogyne* resistant cotton have been shown previously (Ogallo et al., 1999), and are similar to rotations with non-host or poor-host crops.

A study evaluating the multi-year effects of growing a moderately resistant cotton genotype has recently been concluded (R. F. Davis, unpublished). The objective of the study was to document the cumulative effect of moderate resistance on nematode population density and yield loss when a moderately resistant genotype was grown continuously for several years. Highly resistant means that the nematode produces less than 10% of the eggs produced on a susceptible standard; moderate resistance means the nematode produces significantly fewer eggs than on a susceptible standard, but more than 10% of the level on the susceptible standard (Hussey and Janssen, 2002). Three genotypes with differing levels of nematode resistance were grown in Tifton, GA: CPCSD Acala NemX is highly resistant with more than 90% suppression (Ogallo et al., 1997; Ogallo et al., 1999), but it is not adapted to the Southeast; Phytogen Seed Company PH98-3196 is moderately resistant with 80 to 90% suppression (R. F. Davis, unpublished); and Delta and Pine Land Company Deltapine DP458 B/R (susceptible standard in this study). Each genotype was grown in both fumigated (1,3-dichloropropene @ 56 l/ha) and non-fumigated plots so that yield loss due to nematodes could be measured. Each genotype and nematicide combination was used in the same place for three seasons so that the cumulative effects could be documented. This study was conducted at two sites. The first year at site A was 2003, and the first year at site B was 2004. In 2006, following three years of the different genotypes, all plots at site A were planted with the susceptible DP458 B/R to document residual effects of planting resistant genotypes.

Nematode population densities in the soil (Figure 3) and root galling (Figure 4) were significantly lower, and percentage yield suppression was numerically lower (data not shown), after moderately resistant cotton compared to the susceptible standard in both fields in all three years. The effect of a moderately resistant genotype was similar to the effect of a highly resistant genotype. The short-term benefit of resistance is that it reduces damage in the current season's crop through reduced galling and lower percentage yield suppression. The longer-term benefit of resistance is that it reduces the nematode pressure in a field, thereby reducing the damage potential for the next year's crop. Differences between susceptible and moderately resistant genotypes are established quickly (after only one season) and then maintained at similar levels in subsequent years. Growing genotypes with a lower level of resistance than PSC 3196 might demonstrate a cumulative benefit after several years. These results show that moderately resistant cotton genotypes are much more beneficial than previously believed and should be pursued for their significant contribution to nematode management.

LIMITATIONS OF HOST-PLANT RESISTANCE

Host-plant resistance to the southern root-knot nematode does not impart resistance to other nematode genera. Therefore, a grower may still need to use a nematicide in fields infested with other damaging nematodes (e.g, *Rotylenchulus reniformis* or *Hoplolaimus columbus*). There also is a risk that, in the absence of suppression by nematicides, other plant-parasitic nematodes may emerge as pests of cotton.

Currently, there are two sources of root-knot nematode resistance being used by cotton breeders: resistance derived from the Auburn 623 RNR germplasm line and resistance in the Acala NemX cultivar. It has not yet been determined whether those sources of resistance are due to the same or different genes: the genes are both located on the same section of chromosome 11, but their inheritance appears to be different (McPherson et al., 2004; Shen et al., 2006; Shepherd, 1974; Wang et al., 2006; and Zhou et al., 1999). Moderately resistant cultivars such as Stoneville LA 887 and related lines derived their resistance from Clevewilt 6, one of the parents of Auburn 623 RNR, and therefore probably do not contain resistance genes other than those found in Auburn 623 RNR. Selection pressure exerted by nematode-resistant genotypes may lead to nematode populations which are better able to reproduce on the resistant plants. There is evidence that this may have started to occur when resistant lines were grown continuously for several years in California (Ogallo, et al, 1997; Roberts, 1995), though growing NemX continuously for three years did not increase nematode virulence (Ogallo et al., 1999). Preventing the loss of efficacy of resistance genes will require resistance-gene deployment strategies that minimize selection pressure on nematode populations. Additional sources of resistance will be invaluable in prolonging the effectiveness of root-knot nematode resistance in cotton.

Breeding cotton for resistance to root-knot nematodes has been very labor-intensive and difficult. Recent work has identified DNA markers linked to root-knot nematode resistance in cotton (Shen et al, 2006; Wang et al., 2006). Additional advances in this area should allow breeders to use markers to help select nematode-resistant genotypes in large-volume, commercial breeding programs. The genetic basis for tolerance in cotton has not been described, and no genes imparting tolerance (other than resistance genes) have been identified.

When genes conferring a desirable trait (e.g., resistance) are introgressed from an inferior genotype (e.g., a race stock or related wild species) into a crop, DNA near the desirable gene but conferring deleterious traits may also be incorporated. Accidental incorporation of deleterious DNA is called linkage drag; if it reduces yield, it is called yield drag. However, suspected yield drag may be due not to linkage drag but to incorporating the desired gene into a genotype that has lower yield potential (Martin and Hyde, 2001). The nematode-resistant Acala NemX had a lower yield potential than the susceptible cultivar Maxxa at very low nematode levels (Ogallo et al. 1999), but it cannot be concluded whether that difference is due to yield drag or simply to cultivar differences.

Figure 1. Relationship of yield suppression and *Meloidogyne incognita* reproduction on selected cotton genotypes. Each data point is a mean value for a single genotype from two tests (12 observations for reproduction and six observations for yield suppression) (from Davis and May, 2003).

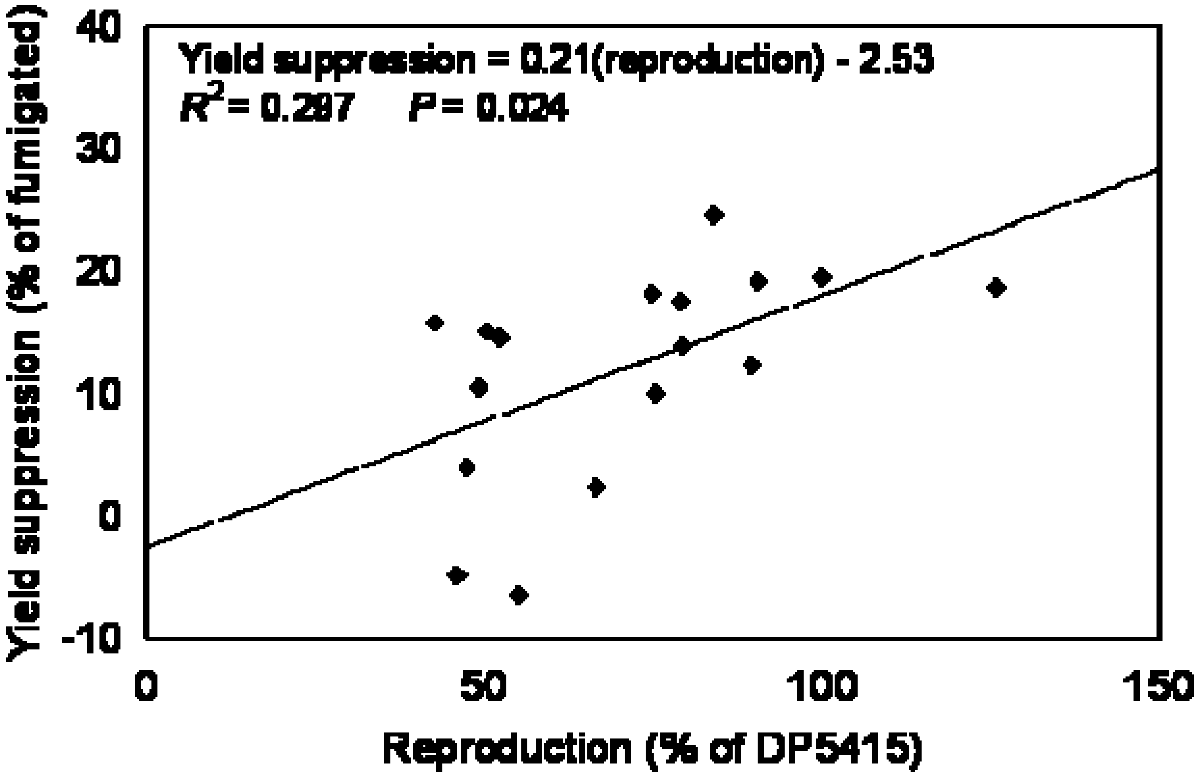


Figure 2. The relationship between yield potential of cotton and percentage yield suppression caused by *Meloidogyne incognita* in Tifton, Georgia in 2002 and 2003 (from Davis and May, 2005).

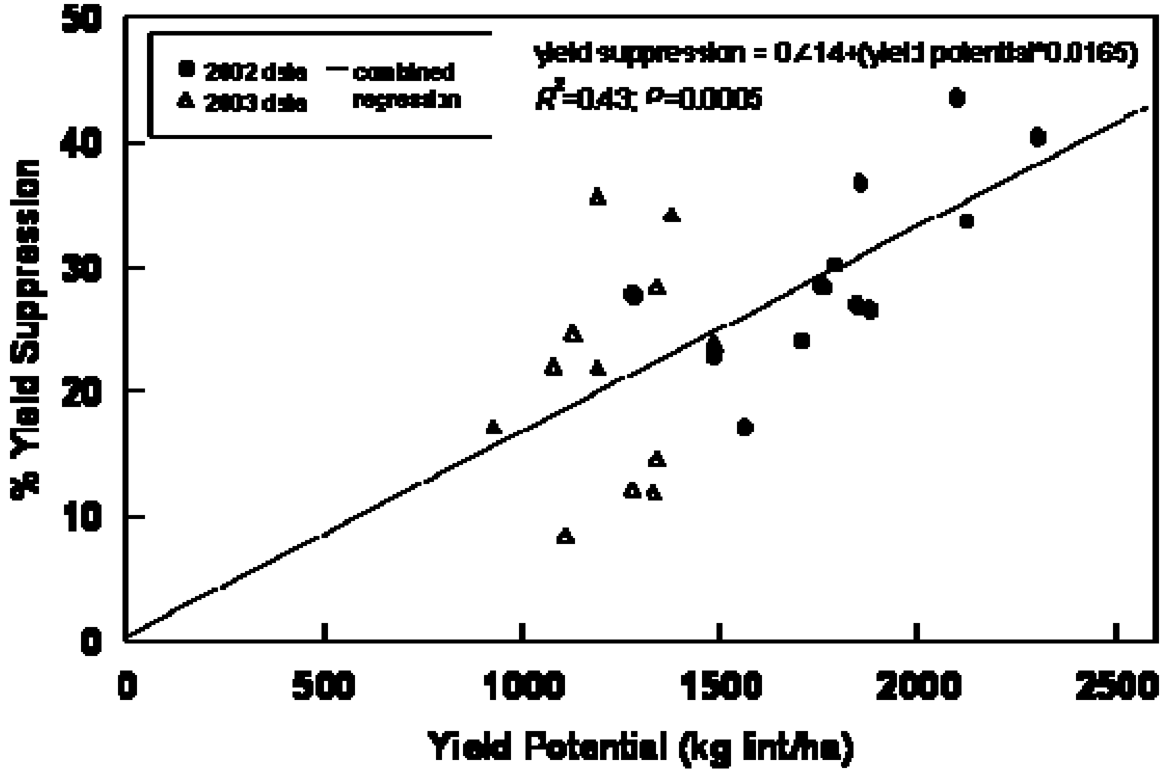
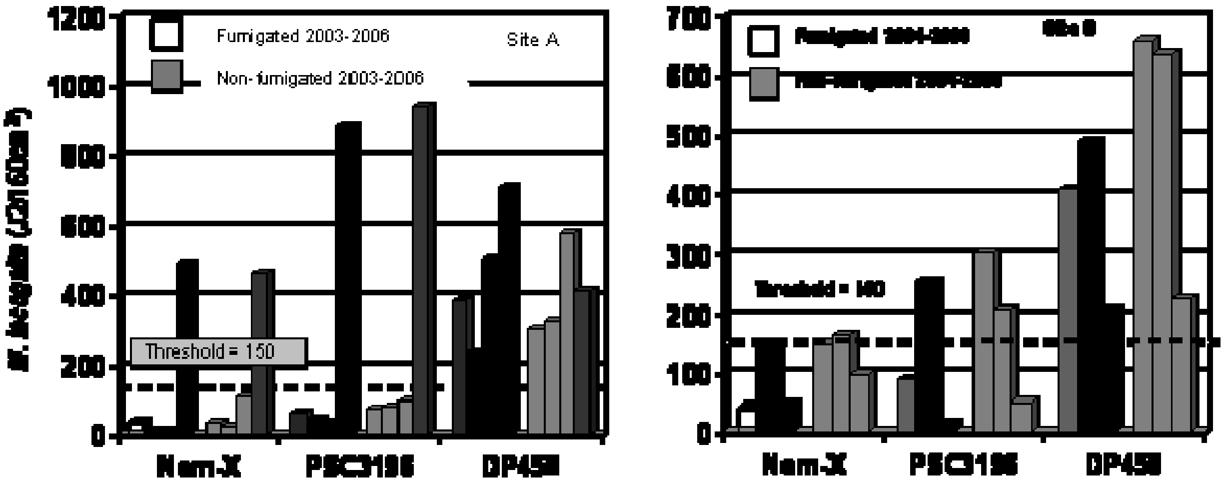


Figure 3. Effect of high (Nem-X), moderate (PSC3196), or no resistance (DP458) on end-of-season population densities of *M. incognita* at two field sites (A and B). In the fourth year (2006) at field site A, all plots were planted with the susceptible DP458 regardless of the previously planted genotype. Bars are striped or solid to denote fumigation and shaded more darkly to denote the fourth year at site A with all plots planted with the susceptible standard.



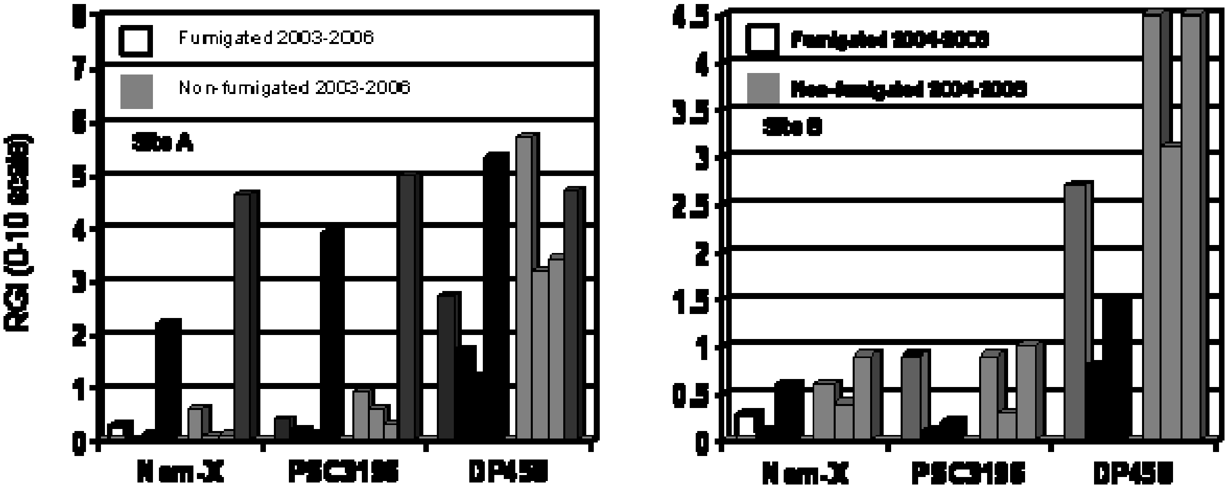


Figure 4. Effect of high (Nem-X), moderate (PSC3196), or no resistance (DP458) on end-of-season root gall indices when grown for three consecutive years at two field sites (A and B). In the fourth year (2006) at field site A, all plots were planted with the susceptible DP458 regardless of the previously planted genotype, so bars are striped or solid to denote fumigation and shaded more darkly to differentiate them from previous years.

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