

RESISTANCE MECHANISMS OF SOUTH AFRICAN SUGARCANE TO THE STALK BORER *ELDANA SACCHARINA* (LEPIDOPTERA: PYRALIDAE): A REVIEW

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Despite plant resistance constituting one of the major defences of South African sugarcane against the stalk borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Leslie and Keeping, 1996; Keeping, 1999; Keeping and Govender, 2002), little has been published regarding the mechanisms upon which this resistance is based. This paper reviews published and unpublished information on this subject, in an attempt to synthesise our understanding of the major resistance mechanisms against *E. saccharina*.

The first line of plant defence – ovipositional antixenosis – is apparently unimportant in the *E. saccharina*-sugarcane interaction. Several studies (Nuss and Atkinson, 1983; Mabulu and Keeping, 1999; Anon, 2003) using potted sugarcane of resistant and susceptible varieties placed in cages in a glasshouse, yielded no evidence that mated female moths preferred certain varieties over others for oviposition. Therefore, it appears that resistance is largely, if not entirely, based on the reaction of the larval stages to physico-chemical factors both on the outside and inside of stalks.

Leslie (1993) found that penetration of stalks by neonate larvae in the field over the first four days following eclosion was substantially delayed in a resistant variety (N8) compared with two susceptible varieties (NCo376 and N11), with the majority of larvae on N8 being recovered from dead leaf sheaths rather than cracks, buds or root bands, as in the susceptible varieties. Percentage recoveries also dropped steeply within the first days following eclosion. Mabulu (2002) found that within seven days approximately 30% of neonates could be recovered from a resistant variety (N21), while 90% could be recovered from a susceptible variety (N11). Similar trends were recorded in field and cage studies using other resistant and susceptible varieties (unpublished data¹).

These results provided the first quantitative evidence for larval antixenosis and early stage antibiosis as resistance mechanisms of sugarcane against *E. saccharina*. Previous studies have demonstrated that a large proportion of dispersing *E. saccharina* neonates suffer mortality due to predation (especially by ants) and other natural causes (Girling, 1978; Leslie, 1988, 1993). Early stage larval antixenosis/antibiosis producing increased larval mobility and delayed stalk penetration results in longer exposure of larvae to natural or applied mortality factors. Indirectly, therefore, it represents the sugarcane plant's major defence against *E. saccharina* and has been identified as the major mechanism of resistance of NCo310 and other resistant varieties to the pyralid borer *Diatraea saccharalis* (F) in Louisiana (Kyle and

¹ GW Leslie, The Behaviour of Young Larvae, File: 8.1.53, Folios 86, 88, 102, 111. Internal Report, South African Sugar Association Experiment Station, Mount Edgecombe, South Africa.

Hensley, 1970). Its great advantage is that it reduces damage to the plant from the outset, rather than acting on the insect only after it has commenced internal feeding.

Several plant characters probably contribute to larval antixenosis and early stage antibiosis. Internode rind hardness is important in resistance to sugarcane borers elsewhere in the world (Kyle and Hensley, 1970; David and Joseph, 1984) and is apparently so with respect to *E. saccharina*. In a field trial experimentally infested with *E. saccharina* and containing 72 varieties of widely varying resistance/susceptibility, internode rind hardness was significantly negatively correlated with number of internodes bored ($r=-0.439$, $p<0.001$), borer numbers ($r=-0.396$; $p<0.001$) and borer mass ($r=-0.323$, $p<0.001$) per stalk (Anon, 2001). Rind hardness is, however, significantly correlated with fibre % cane ($r=0.588$, $p<0.001$, $n=81$ varieties), as is fibre % cane with *E. saccharina* resistance (Rutherford *et al.*, 1993). Hence, although rind hardness may be a good character for imparting plant resistance, its association with fibre and the well-established negative relationship between fibre % cane and recoverable sucrose (King, 1989; Brokensha, 1996), make it undesirable as a selection trait for resistance to the borer. Although high sucrose yielding varieties have previously been considered as more susceptible to *E. saccharina* (Nuss *et al.*, 1986), recently released resistant varieties (e.g. N29, N39, N41) are also relatively high in recoverable sucrose with only moderate fibre content, indicating that resistance in these varieties is influenced less by physical toughness of the stalk and more by plant chemistry and physiological reaction to damage.

The plant surface is a critical interface between insects and plants, and especially interesting but understudied in this regard are surface waxes. Besides their role in preventing plant desiccation in water-limiting environments (Riederer and Schreiber, 2001), surface waxes may protect plants from pathogens (Jenks *et al.*, 1994; Carver *et al.*, 1996) and insects (Eigenbrode and Espelie, 1995). Both the quantity (Mathes and Charpentier, 1969) and chemical composition of epicuticular stalk waxes may be associated with larval antixenosis or early stage antibiosis of sugarcane to stalk borers. A high ratio of the C30 alcohol, triacontanol, to C30 aldehyde appears to be associated with resistance to *E. saccharina* (Rutherford and van Staden, 1996). Triacontanol is known to influence the behaviour of insects on other plants. For example, *Arabidopsis* mutant Cer3 waxes have notably increased triacontanol contents. This causes increased mobility and reduced host-plant acceptance by the cabbage aphid *Brevicoryne brassicae* (Rashotte *et al.*, 1997; Rashotte, 1999).

The observation that *E. saccharina* larvae most commonly penetrate the stalk via the node, and in particular the bud (Atkinson, 1980), is consistent with the hypothesis that the chemical composition of budscale flavonoids and chlorogenates is involved in early stage antibiosis, when young larvae bore into and feed on the bud. Two extreme types of flavonoid compositions have been found, one associated with resistance and the other with susceptibility (Rutherford, 1998).

Resistance to sugarcane smut is also partially determined by pre-formed bud flavonoids (Lloyd and Naidoo, 1983). Surface wax components may also be involved in smut resistance. James (1973) reported a significant correlation between percentage smut spore germination on the wax of the internode surface and varietal resistance ratings ($r=+0.728$; $p<0.001$). It therefore appears that bud and surface wax chemistry can contribute towards resistance to both *E. saccharina* and smut. Unfortunately the two traits are negatively correlated (Heinze *et al.*, 2001).

Significant differences in growth (mass) of larvae and pupae, as well as subsequent stalk damage, in commercial and unreleased sugarcane clones planted in field (Keeping, 1999) and potted cane screening trials (Keeping and Govender, 2002), indicate that antibiosis following stalk penetration is also an important resistance mechanism. However, differences in survival among larvae feeding internally on stalks of resistant and susceptible varieties are unlikely to be as marked as during the early stages of larval establishment, although this has yet to be demonstrated. Other than fibre and possible internal chemical differences between varieties, stalk silicon (Si) content and Si-accumulating capacity differ between *E. saccharina*-resistant and susceptible varieties. Although the mechanism has yet to be elucidated, Si increases resistance of sugarcane to *E. saccharina* (Keeping and Meyer, 2002, 2003).

Gene expression and molecular marker studies suggest that physiological reaction to damage differs between resistant and susceptible sugarcane varieties. Heinze *et al.* (2001) set out to identify genes that are differentially expressed in response to damage by *E. saccharina*. Differentially expressed genic fragments have the potential to be useful in marker assisted breeding once a link with resistance has been confirmed, for example by Restriction Fragment Length Polymorphism. A number of marker combinations have been identified which suggest an important role for flavonoids and protease inhibitors in resistance to *E. saccharina*.

Of the six commercial varieties resistant to *E. saccharina*, four (N12, N21, N33, N39) have good drought tolerance and two (N29, N41) average drought tolerance, while only three of the remaining 23 commercial varieties have good drought tolerance (10 of these have poor tolerance). Extensive evidence indicates that water stress promotes outbreaks of phytophagous insects. Three hypotheses have been put forward to explain this. First, drought increases insect survival and growth through elevated plant nutrient levels, especially nitrogen (White, 1984; Atkinson and Nuss, 1989). Secondly, the plant's ability to defend itself is reduced, and thirdly, a more suitable physical environment, especially increased plant temperature, is provided (Rhoades, 1983).

Finally, tolerance to insect herbivore damage, wherein a host plant is able to compensate for losses caused by a pest, remains to be investigated as a resistance mechanism of sugarcane to *E. saccharina*.

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