Bulletin of Entomological Research (2008) **98**, 355–359
doi:10.1017/S0007485308005658

First published online 18 February 2008
Printed in the United Kingdom

Stability of spinosad resistance in *Frankliniella occidentalis* (Pergande) under laboratory conditions

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Abstract

The stability of spinosad resistance in western flower thrips (WFT), *Frankliniella occidentalis* (Pergande), populations with differing initial frequencies of resistance was studied in laboratory conditions. The stability of resistance was assessed in bimonthly residual bioassays in five populations with initial frequencies of 100, 75, 50, 25 and 0% of resistant individuals. There were no consistent changes in susceptibility of the susceptible strain after eight months without insecticide pressure. In the resistant strain, very highly resistant to spinosad ($RF_{50} > 23{,}000$-fold), resistance was maintained up to eight months without further exposure to spinosad. In the absence of any immigration of susceptible genes into the population, resistance was stable. In the case of the population with different initial frequency of resistant thrips, spinosad resistance declined significantly two months later in the absence of selection pressure. With successive generations, these strains did not change significantly in sensitivity. Spinosad resistance in *F. occidentalis* declined significantly in the absence of selection pressure and the presence of susceptible WFT. These results suggest that spinosad resistance probably is unstable under field conditions, primarily due to the immigration of susceptible WFT. Factors influencing stability or reversion of spinosad resistance are discussed.

Keywords: Thysanoptera, insecticide-resistance, stability, spinosad, spinosyns

(Accepted 14 September 2007)

Introduction

The western flower thrips (WFT), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is an economically important pest of vegetable, fruit and ornamental crops throughout the world, primarily due to its role as virus vector. Due to the low damage threshold on some crops, especially in Tomato Spotted Wilt Virus susceptible crops, the most widely used method of WFT control is through the application of insecticides. However, the indiscriminate use of insecticides, the short generation time of *F. occidentalis*, its high fecundity and the haplodiploid breeding system, in which resistance genes are directly exposed to selection by insecticide treatment, have led to the development of resistance to major insecticide groups: organochlorines, organophosphates, carbamates, pyrethroids and spinosyns (Immaraju *et al*., 1992; Brødsgaard, 1994; Martin & Workman, 1994; Robb *et al*., 1995; Zhao *et al*., 1995; Broadbent & Pree, 1997; Espinosa *et al*., 2002a; Herron & James, 2005; Bielza *et al*., 2007a).

Spinosad is the first member of the Spinosyns group 5 Nicotinic Acetylcholine receptor agonists (allosteric) according to IRAC (Insecticide Resistance Action Committee) mode of action classification (Anonymous, 2005), developed by

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Dow AgroSciences (Sparks *et al.*, 1995). In Spain, spinosad is widely used for the control of lepidopteran and thysanopteran pests after being introduced in 2002, with excellent initial control of *F. occidentalis*. Due to this high efficacy for thrips control and severe resistance problems with other insecticides (Espinosa *et al.*, 2002a,b, 2005), for most growers spinosad became almost the only insecticide used against WFT in some areas. Spinosad overuse, with more than ten applications per crop, has produced highly resistant populations in some greenhouses of southeastern Spain (Bielza *et al.*, 2007a), an area of very intensive insecticide use. However, field rates of spinosad provide good WFT control in most greenhouses where spinosad is used judiciously.

Metabolic mediated detoxification was not responsible for spinosad resistance (Bielza *et al.*, 2007a), in contrast with the resistance mechanism for other insecticides used against thrips – mediated by esterases (Maymó *et al.*, 2006) or, mainly, by monooxygenases (Espinosa *et al.*, 2005). These results explain the lack of cross-resistance with the other insecticides used against thrips (Bielza *et al.*, 2007a).

To preserve the usefulness of spinosad in *F. occidentalis* management, it is important to identify effective strategies for the development of a comprehensive resistance management program to retard the progress of spinosad resistance in the field.

An important component of resistance management is the rotational use of insecticides which do not show cross-resistance (Ninsin & Tanaka, 2005). A key assumption for an effective rotation strategy is that the frequency of resistant individuals will decline during the application of an alternate insecticide (Tabashnik, 1990). When an insecticide is withdrawn, susceptibility of the insect will be restored within several generations, thus allowing the insecticide to be re-incorporated into pest-management programs. However, in certain cases, resistance persists over many generations after the withdrawal of selection pressure (Nauen *et al.*, 2002). Since stable resistance prevents the successful re-use of an insecticide for pest management, a study on the stability of spinosad resistance in *F. occidentalis* in the absence of further selection was conducted.

Material and methods

Insect strains

The susceptible strain (S) of *F. occidentalis* was collected in 2001 (the year before spinosad introduction) from sweet pepper crops in Murcia (Bielza *et al.*, 2007a). This strain was maintained in the laboratory (Espinosa *et al.*, 2002c) without outside gene flow or exposure to insecticide.

In 2003, six *F. occidentalis* strains were collected in Almeria (Spain) from greenhouses with an intense previous use of spinosad (>10 applications in six months), where resistant problems were suspected (Bielza *et al.*, 2007a). These field populations of *F. occidentalis* were reared and bioassayed against spinosad, and survivors from doses above the lethal concentration 50 (LC_{50}) were pooled and reared. The resulting population was exposed each month (approximately each generation) to increasing concentrations of spinosad over four months. This selected strain (R) for resistance to spinosad was maintained isolated in the laboratory.

Insecticides

A commercial formulation of spinosad (Spintor® 480 g spinosad l^{-1}, Dow AgroSciences) was used in bioassays. Tests solutions of spinosad were freshly prepared in distilled water with Tween 20 (1‰) as surfactant.

Bioassays

Leaf-dip bioassays were conducted on one-week-old female adults of *F. occidentalis*. Sweet pepper leaf sections (30×5 mm) were immersed for 10 s in the test solution and then allowed to dry for 1–2 h at room temperature. Control leaf sections were immersed in distilled water containing Tween 20 (1‰). The leaf sections were then transferred to new individual plastic vials (5 ml). Ten female adult thrips were placed into each vial. The vials were closed with a piece of cellulose paper below the cap to prevent water condensation and were maintained in the vertical position at 25 ± 2°C and a photoperiod of 16:8 h (light : dark). Five to nine concentrations, plus a control (without insecticide), were assayed for each population in three replications containing ten adult thrips per dose. Doses (between 0.0061 and 101990.4 mg spinosad l^{-1}) were chosen to give a range of 0–100% mortality. This was assessed after 24 h, individuals which did not move were scored as dead.

Stability of resistance

Spinosad toxicity was evaluated bimonthly in five populations with different initial percentage (100, 75, 50, 25 and 0%) of resistant thrips. These populations were initiated using different proportions of WFT from the selected resistant (R) and the susceptible (S) populations of *F. occidentalis*. Each population was kept on green bean pods, in plastic containers (19 cm tall and 11 cm dia.) (Espinosa *et al.*, 2002c, Espinosa *et al.*, 2005). The containers were maintained under 25 ± 1°C and 16:8 h light : dark photoperiod. At this temperature, the duration of the developmental period (egg to adult) and the mean generation time of *F. occidentalis* were around 16 and 24 days, respectively. The initial population (R + S) in each cage contained at least 400 larvae thrips.

Data analysis

Data were analyzed using the program POLO-PC (Russell *et al.*, 1977) for Probit analysis. The lethal concentrations (LC_{50} and LC_{90}) plus their 95% fiducial limits were calculated. Resistance factors (RF) at the LC_{50} or LC_{90} level (RF_{50} and RF_{90}), plus their associated 95% confidence intervals (CI), were calculated as outlined in Robertson & Preisler (1992).

Results and discussion

As would be expected, there were no consistent changes in susceptibility of the susceptible strain (S: 0 r + 100 s), up to eight months without insecticide pressure (table 1).

In the resistant strain (R: 100 r + 0 s), that was highly resistant to spinosad (RF_{50} > 23,000-fold), resistance was maintained up to eight months without further exposure to spinosad (tables 1 and 2). Apparently, the resistant strain was highly homogenous with the predominant genotype,

https://doi.org/10.1017/S0007485308005658 Published online by Cambridge University Press

Table 1. Slopes and lethal concentrations (LC) of spinosad in *Frankliniella occidentalis* populations with initial frequencies of 0, 25, 50, 75 and 100% of resistant individuals, tested bimonthly over an eight month period.

Strain	Month	Slope (±SE)	LC_{50} (mg liter^{-1}) (95% FL)	LC_{90} (mg liter^{-1}) (95% FL)
0 r + 100 s	0	1.18 (±0.16)	0.42 (0.24–0.73)	5.20 (2.64–14.24)
	2	1.49 (±0.19)	0.28 (0.18–0.44)	2.04 (1.19–4.47)
	4	1.28 (±0.19)	0.47 (0.28–0.77)	4.78 (2.55–12.72)
	6	1.01 (±0.12)	0.35 (0.22–0.59)	6.51 (3.08–20.02)
	8	1.42 (±0.23)	0.27 (0.14–0.44)	2.16 (1.22–5.27)
25 r + 75 s	2	1.50 (±0.29)	2.36 (1.32–3.79)	16.98 (9.20–54.58)
	4	1.05 (±0.22)	2.72 (1.32–5.20)	45.16 (17.71–343.07)
	6	1.09 (±0.15)	3.35 (2.05–5.93)	50.53 (22.50–184.19)
	8	0.97 (±0.14)	3.94 (2.30–7.59)	82.30 (32.09–387.55)
50 r + 50 s	2	0.59 (±0.09)	2.93 (1.18–7.64)	420.64 (101.43–4606.80)
	4	0.60 (±0.10)	1.92 (0.60–5.65)	260.38 (51.21–9014.50)
	6	0.92 (±0.11)	7.45 (4.38–13.65)	185.67 (76.58–725.21)
	8	0.84 (±0.10)	5.22 (2.99–9.58)	172.51 (69.29–697.37)
75 r + 25 s	2	0.66 (±0.12)	114 (27–333)	10 364 (2857–103 370)
	4	0.81 (±0.17)	59 (25–141)	2274 (656–31 678)
	6	0.54 (±0.07)	75 (35–164)	16 948 (4481–140 660)
	8	0.55 (±0.09)	116 (43–289)	25 361 (5888–348 160)
100 r + 0 s	0	1.43 (±0.25)	16 385 (9717–26 618)	129 420 (68 047–408 950)
	2	1.44 (±0.20)	12 368 (8185–19 205)	96 075 (52 771–248 430)
	4	1.19 (±0.19)	11 044 (6292–19 084)	132 520 (62 982–474 720)
	6	1.37 (±0.19)	14 827 (9695–23 792)	127 210 (66 361–364 900)
	8	1.46 (±0.20)	14 734 (9788–23 051)	110 810 (60 399–292 570)

Table 2. Resistant factors (95% confidence intervals) at lethal concentration 50 level towards spinosad in *F. occidentalis* populations with initial frequencies of 0, 25, 50, 75 and 100% of resistant individuals, tested bimonthly during eight months.

Strain	Month				
	0	2	4	6	8
0 r + 100 s	1.0	0.7 (0.3–1.4)	1.1 (0.5–2.4)	0.8 (0.4–1.8)	0.6 (0.3–1.4)
25 r + 75 s		8.4 (4.3–16.4)	5.7 (2.5–12.9)	9.5 (4.6–19.6)	14.6 (6.6–32.3)
50 r + 50 s		10.4 (3.8–28.8)	4.1 (1.5–11.0)	21.1 (9.9–44.7)	19.4 (8.8–42.6)
75 r + 25 s		406 (114–1442)	125 (48–326)	211 (85–523)	430 (149–1246)
100 r + 0 s	38,765 (18,561–80,959)	44,245 (23,954–81,725)	23,198 (11,090–48,525)	41,976 (21,550–81,764)	54,538 (27,515–108,099)

rr (Bielza *et al*., 2007b). In the absence of any immigration of susceptible genes into the population, resistance was stable for this period of time. These results could suggest that there are no significant biological disadvantages to a highly resistant lab-reared WFT population containing a low frequency of susceptible individuals. Similarly, when a highly resistant strain (RF = 669-fold) of *Heliothis virescens* (F.) (Lepidoptera: Noctuidae), selected in the laboratory for 13 generations, was not exposed to spinosad for five generations, only minor reversion (1.4-fold) to susceptibility was observed (Wyss *et al*., 2003).

Many authors have shown that resistance is not necessarily eliminated by the cessation of pesticide treatments in *F. occidentalis*. Robb (1989) identified a strain which retained resistance to dimethoate seven years after exposure. Brøadsgaard (1994) obtained a moderate level of resistance to acephate (RF = 95-fold), after 100 generations without selection pressure. Kontsadalov *et al*. (1998) found cipermethrin resistance in a WFT lab strain reared for seven years in isolated conditions, without insecticide pressure. In a previous work (Contreras *et al*., in press), a WFT laboratory strain, very highly resistant to acrinathrin (RF > 1000-fold), maintained the resistance up to eight months without further exposure to the insecticide.

When susceptible thrips were mixed with resistant thrips in the different strains (75 r + 25 s, 50 r + 50 s, 25 r + 75 s), the resistance to spinosad declined significantly in the presence of susceptible thrips (tables 1 and 2). In the case of the population with an initial frequency of 75% of resistant thrips (75 r + 25 s), spinosad resistance declined significantly two months after the mixing, in the first bioassay assessed, in the absence of selection pressure (RF_{50} = 406, table 2). However, the rate of decline was slower than in the populations with the lowest initial percentages of resistant thrips (50 r + 50 s, 25 r + 75 s). With successive generations, this strain did not change significantly in sensitivity and had a resistant factor of 125–430.

For the populations with an initial resistance frequency of 50% and 25% (50 r + 50 s, 25 r + 75 s), LC_{50} values decreased dramatically two months later (around two generations), with RF_{50}s 8.4–10.4-fold, after the mixing with susceptible thrips (tables 1 and 2). With successive generations, these

https://doi.org/10.1017/S0007485308005658 Published online by Cambridge University Press

Table 3. Resistant factors (95% confidence intervals) at lethal concentration 90 level towards spinosad in *F. occidentalis* populations with initial frequencies of 0, 25, 50, 75 and 100% of resistant individuals, tested bimonthly during eight months.

Strain	Month				
	0	2	4	6	8
0 r + 100 s	1.0	0.4 (0.1–1.1)	0.9 (0.3–2.8)	1.3 (0.4–4.2)	0.4 (0.1–1.2)
25 r + 75 s		8.3 (3.0–23.2)	9.4 (2.1–41.9)	7.7 (2.0–30.0)	37.9 (9.6–149.2)
50 r + 50 s		205.9 (30.4–1392.3)	54.5 (7.5–398.2)	28.4 (6.9–117.0)	79.3 (21.4–294.5)
75 r + 25 s		5048 (875–29125)	476 (74–3046)	2582 (392–17019)	11,630 (1560–86,723)
100 r + 0 s	24,909 (7838–79,163)	47,395 (17,754–126,525)	27,576 (8197–92,770)	19,518 (5777–65,949)	51,010 (18,382–141,551)

strains did not change significantly in sensitivity and had a resistant factor of 4.1–21.1.

Reversion to a more susceptible condition occurred very rapidly, in the first bioassay assessed two months later (*ca*. two generations). This is supported by the findings of Ferguson (2004), who reported a reversion of spinosad resistance over just one to three generations in field-collected populations of *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae). Field strains are more heterogeneous than laboratory strains owing to a bigger gene pool in field than in laboratory selections (Keiding, 1986). Individual field insects do not always receive sufficient exposure to insecticides; and, therefore, susceptible thrips can survive, resulting in field populations with susceptible and resistant individuals, as in our laboratory mixed populations.

Although a study in field conditions is required, our lab results suggest that spinosad resistance would not be stable under field conditions, in the early generations after the final spinosad treatment. Surviving susceptible individuals and/or immigration of susceptible ones dilute resistance through interbreeding with resistant individuals. The tendency of the resistance would be to fall quickly, particularly in the early generations, until a progressive stability was reached.

According to Roush & Croft (1986), the major factors that influence the rate of reversion are relative fitness differences, initial gene frequencies and the dominance relationships of the resistant and susceptible allele(s) of the phenotypes. The persistence of spinosad resistance in the isolated resistant strain, in an insecticide-free environment, indicates a low fitness cost associated with the resistance mechanism. However, more studies of fitness cost are needed to test such conjectures. Previous results (Bielza *et al*., 2007b) showed that spinosad resistance in *F. occidentalis* is expressed as an almost completely recessive trait, probably controlled by one locus. The recessive nature of spinosad resistance and the apparent lack of fitness cost suggest that the main factor for reversion of spinosad resistance is the immigration of susceptible individuals. Migration occurring locally is very intense in some areas, where thrips spread among weeds, outdoors crops and greenhouses. WFT mobility is higher in plants in which inflorescences have a short life-span, as most vegetable crops.

However, for the populations with an initial frequency of resistant thrips, some level of resistance persists eight months later, even for the population with 25% of resistant thrips ($RF_{50} = 14.6$) (table 1). The mixed populations remained quite heterogeneous for spinosad resistance even after eight months culture, indicated by the high RF_{90} (table 3), particularly in the populations with a higher initial resistance frequency of 50% and 75%, with RF_{90} of 79.3 and 11,630-fold. A population usually takes longer to recover susceptibility than it does to acquire resistance, and resistance will probably remerge significantly faster following the reintroduction of the pesticide (May & Dobson, 1986). There are always a number of resistant survivors that could be selected in the re-use of insecticide pressures (Hoy, 1998; May & Dobson, 1986).

Moreover, there are not many insecticides registered that are effective against *F. occidentalis*, consequently growers have a small pool of unrelated insecticides to rotate. This situation results in considerable selection pressure, a pressure that will rapidly lead to evolution of thrips with even greater resistance to specific insecticides (Brødsgaard, 1994). The problem is made worse because host crops for the pest are in continuous production, and resistant thrips populations from the host crop could migrate to new crops.

In order to mitigate these cases of resistance, an insecticide resistance management (IRM) strategy was implemented for greenhouse crops, consisting of insecticide rotation between resistance mechanisms (Espinosa *et al*., 2005; Bielza *et al*., 2007a), but with a limited number of spinosad applications per crop. Dow AgroSciences, the manufacturer of spinosad, recommends an IRM strategy that limited spinosad use to a maximum of three applications per crop.

The evolution of resistance can be described by considering both genetic and ecological factors (Roush & Croft, 1986). We have shown in this report that resistance in *F. occidentalis* to spinosad declined significantly in the absence of selection pressure and the presence of susceptible thrips. These results suggest that spinosad resistance probably is unstable in field conditions, mainly due to the immigration of sensitive thrips. This unstable resistance implies that the rotational use of spinosad with other insecticides, such as acrinathrin, methiocarb and formetanate, that do not show cross-resistance (Espinosa *et al*., 2005; Bielza *et al*., 2007a) would be an effective approach in maintaining susceptible individuals in field populations of *F. occidentalis* so as to further retard the development of insecticide resistance.

However, it is clear that more investigation is needed in this area in order to further appreciate the pattern of evolution of spinosad resistance in the field and the fitness cost of the maintaining spinosad resistance in WFT populations over time.

Acknowledgements

We acknowledge anonymous referees for reviews and comments on the manuscript. This research has been supported by the Spanish Ministry of Education and Science – CICYT (AGL2005-07492-C02-01). The project was partly supported by Dow AgroSciences.

References

Anonymous (2005) IRAC Mode of Action Classification. http://www.irac-online.org.

Bielza, P., Quinto, V., Contreras, J., Torné, M., Martín, A. & Espinosa, P.J. (2007a) Resistance to spinosad in the western flower thrips, *Frankliniella occidentalis* (Pergande), in greenhouses of southeastern Spain. *Pest Management Science* **63**, 682–687.

Bielza, P., Quinto, V., Fernández, E., Grávalos, C. & Contreras, J. (2007b) Genetics of spinosad resistance in *Frankliniella occidentalis* (Thysanoptera: Thripidae). *Journal of Economic Entomology* **100**, 916–920.

Broadbent, A.B. & Pree, D.J. (1997) Resistance to insecticides in populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) from greenhouses in the Niagara Region of Ontario. *Canadian Entomologist* **129**, 907–913.

Brødsgaard, H.F. (1994) Insecticide resistance in European and African strains of western flower thrips (Thysanoptera: Thripidae) tested in a new residue-on-glass test. *Journal of Economic Entomology* **87**, 1141–1146.

Contreras, J., Espinosa, P.J., Quinto, V., Grávalos, C., Fernández, E. & Bielza, P. (???) Stability of insecticide resistance in *Frankliniella occidentalis* (Pergande) to acrinathrin, formetanate and methiocarb. *Agricultural and Forest Entomology*, in press.

Espinosa, P.J., Bielza, P., Contreras, J. & Lacasa, A. (2002a) Field and laboratory selection of *Frankliniella occidentalis* (Pergande) for resistance to insecticides. *Pest Management Science* **58**, 920–927.

Espinosa, P.J., Bielza, P., Contreras, J. & Lacasa, A. (2002b) Insecticide resistance in field populations of *Frankliniella occidentalis* (Pergande) in Murcia (south-east Spain). *Pest Management Science* **58**, 967–971.

Espinosa, P.J., Fuentes, J.F., Contreras, J., Bielza, P. & Lacasa, A. (2002c) Método de cría en masa de *Frankliniella occidentalis* (Pergande). *Boletín de Sanidad Vegetal: Plagas* **28**, 385–390.

Espinosa, P.J., Contreras, J., Quinto, V., Grávalos, C., Fernández, E. & Bielza, P. (2005) Metabolic mechanisms of insecticide resistance in the western flower thrips, *Frankliniella occidentalis* (Pergande). *Pest Management Science* **61**, 1009–1015.

Ferguson, J.S. (2004) Development and stability of insecticide resistance in the leafminer *Liriomyza trifolii* (Diptera: Agromyzidae) to cyromazine, abamectin, and spinosad. *Journal of Economic Entomology* **97**, 112–119.

Herron, G.A. & James, T.M. (2005) Monitoring insecticide resistance in Australian *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) detects fipronil and spinosad resistance. *Australian Journal of Entomology* **44**, 299–303.

Hoy, M.A. (1998) Myths models and mitigation of resistance to pesticides. *Philosophical Transactions of the Royal Society of Londo, Series B: Biological Sciences* **353**, 1787–1795.

Immaraju, J.A., Paine, T.D., Bethke, J.A., Roob, K.L. & Newman, J.P. (1992) Western flower thrips (Thysanoptera: Thripidae) resistance to insecticides in costal California greenhouses. *Journal of Economic Entomology* **85**, 9–14.

Keiding, J. (1986) Prediction or resistance risk assessment. pp. 279–297 *in* National Research Council (*Ed.*) *Pesticide Resistance Strategies and Tactics for Management*. Washington DC, National Academy Press.

Kontsedalov, S., Weintraub, P.G., Horowitz, A.R. & Ishaaya, I. (1998) Effects of insecticides on immature and adult western flower thrips (Thysanoptera: Thripidae) in Israel. *Journal of Economic Entomology* **91**, 1067–1071.

Martin, N.A. & Workman, P.J. (1994) Confirmation of a pesticide-resistant strain of western flower thrips in New Zealand. pp. 144–148 in *Proceedings of the 47th New Zealand Plant Protection Conference*. 9–11 August 1994, Waitangi Hotel, New Zealand.

May, R.M. & Dobson, A. (1986) Population dynamics and the rate of evolution of pesticide resistance. pp. 170–193 *in* National Research Council (*Ed.*) *Pesticide Resistance Strategies and Tactics for Management*. Washington DC, National Academy Press.

Maymó, A.C., Cervera, A., Garcerá, M.D., Bielza, P. & Martínez-Pardo, R. (2006) Relationship between esterase activity and acrinathrin and methiocarb resistance in field populations of western flower thrips, *Frankliniella occidentalis*. *Pest Management Science* **62**, 1129–1137.

Nauen, R., Stumpf, N. & Elbert, A. (2002) Toxicological and mechanistic studies on neonicotinoid cross resistance in Q-type *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Pest Management Science* **58**, 868–875.

Ninsin, K.D. & Tanaka, T. (2005) Synergism and stability of acetamiprid resistance in a laboratory colony of *Plutella xylostella*. *Pest Management Science* **61**, 723–727.

Robb, K.L. (1989) Analysis of *Frankliniella occidentalis* (Pergande) as a pest of floricultural crops in California greenhouses. PhD thesis, University of California, Riverside, USA.

Robb, K.L., Newman, J., Virzi, J.K. & Parrella, P. (1995) Insecticide resistance in Western Flower Thrips. pp. 341–346 *in* Parker, B.L., Skinner, M. & Lewis, T. (*Eds*) *Thrips Biology and Management*. New York, Plenum Press.

Robertson, J.L. & Preisler, H.K. (1992) *Pesticide Bioassays with Arthropods*. 127 pp. Boca Raton, FL, CRC Press.

Roush, R.T. & Croft, B.A. (1986) Experimental population genetics and ecological studies of pesticide resistance in insects and mites. pp. 257–270 *in* National Research Council (*Ed.*) *Pesticide Resistance Strategies and Tactics for Management*. Washington DC, National Academy Press.

Russell, R.N., Robertson, J.L. & Savin, Y.N.E. (1977) Polo: a new computer program for probit analysis. *Bulletin of the Entomological Society of America* **23**, 209–215.

Sparks, T.C., Thompson, G.D., Larson, L.L., Kirst, H.A., Jantz, O.K., Worden, T.V., Hertlein, M.B. & Busacca, J.D. (1995) Biological characteristics of the spynosyns: a new and naturally derived insect control agent. pp. 903–907 in *Proceedings Beltwide Cotton Conference*. National Cotton Council, 4–7 January 1995, San Antonio, TX.

Tabashnik, B.E. (1990) Modeling and evaluation of resistance management tactics. pp. 153–182 *in* Roush, R.T. & Tabashnik, B.E. (*Eds*) *Pesticide Resistance in Arthropods*. New York, Chapman & Hall.

Wyss, C.F., Young, H.P., Shukla, J. & Roe, R.M. (2003) Biology and genetics of a laboratory strain of the tobacco budworm, *Heliothis virescens* (Lepidoptera: Noctuidae), highly resistant to spinosad. *Crop Protection* **22**, 307–314.

Zhao, G., Liu, W., Brown, J.M. & Knowles, C.O. (1995) Insecticide resistance in field and laboratory strains of western flower thrips (Thysanoptera: Thripidae). *Journal of Economic Entomology* **88**, 1164–1170.