Am. J. Potato Res.
DOI 10.1007/s12230-013-9356-6

Resistance of Selected Potato Genotypes to the Potato Psyllid (Hemiptera: Triozidae)

John Diaz-Montano · Beatriz G. Vindiola · Nichole Drew · Richard G. Novy · J. Creighton Miller Jr · John T. Trumble

Abstract The characterization of resistance of selected potato, *Solanum tuberosum* L., breeding clones to the potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) was investigated. Antixenosis was assessed in choice tests in which a single plant of each genotype was placed inside a rearing cage, where 60 female psyllid adults were released and the number of adults and eggs on each genotype was counted 24 h later. Antibiosis was evaluated in no-choice tests in which adults (five males and five females) were confined in a cage fixed to the upper side of leaves. After 4 h of exposure, adults were removed and the number of eggs counted. The developmental time and survival of offspring were recorded until all insects became adults. All the resistant genotypes showed strong antibiotic effects to *B. cockerelli*. These results show promise for incorporation into an IPM program against *B. cockerelli*.

Resumen Se investigó la caracterización de la resistencia de clones selectos de papa, *Solanum tuberosum* L., al psílido de la papa *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae). Se evaluó la antixenosis en pruebas de selección en las cuales se colocaron plantas individuales de cada genotipo dentro de una jaula de crecimiento, donde se liberaron 60 psílidos adultos hembras y se contó el número de adultos y huevos en cada genotipo 24 h después. Se evaluó la antibiosis en pruebas de no-selección en las cuales los adultos (cinco machos y cinco hembras) se confinaron en una jaula fija en la parte superior de las hojas. Después de cuatro horas de exposición, se retiró a los adultos y se contó el número de huevos. Se registró el tiempo de desarrollo y sobrevivencia de la progenie hasta que todos los insectos se hicieron adultos. Todos los genotipos resistentes mostraron fuertes efectos antibióticos a *B. cockerelli*. Estos resultados son prometedores para la incorporación a un programa de manejo integral (IPM) contra *B. cockerelli*.

Keywords *Bactericera cockerelli* · *Solanum tuberosum* · Antibiosis · Antixenosis

J. Diaz-Montano · B. G. Vindiola · N. Drew · J. T. Trumble
Department of Entomology, University of California, Riverside, CA 92521, USA

R. G. Novy
Small Grains and Potato Germplasm Research Unit, USDA, Agricultural Research Service, 1693 S. 2700 W., Aberdeen, ID 83210, USA

J. C. Miller Jr
Department of Horticultural Sciences, Texas A & M University, College Station, TX 77843, USA

Present Address:
J. Diaz-Montano (✉)
Stored Product Insect Research Unit, USDA, Agricultural Research Service, Center for Grain and Animal Health Research, 1515 College Av., Manhattan, KS 66502-2736, USA
e-mail: john.diaz-montano@ars.usda.gov

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a phloem-feeding pest that causes economic losses to solanaceous vegetables such as tomato, *Solanum lycopersicum* L., pepper, *Capsicum* spp., eggplant, *Solanum melongena* L., and potato, *Solanum tuberosum* L. (Liu and Trumble 2006; Teulon et al. 2009; Butler and Trumble 2012). *Bactericera cockerelli* feeding on potatoes causes retarded growth, chlorosis, small tuber production (Al-Jabr and Whitney 2007) and up to 93 % reduction in yield (Munyaneza et al. 2008). In addition to damage caused by feeding, *B. cockerelli* also transmit the bacterial pathogen "*Candidatus* Liberibacter psyllaurous" (a.k.a. *Ca.* L. solanacearum) that causes an emerging potato disease named zebra chip (ZC) (Hansen et al. 2008; Liefting et al. 2008; Liefting et al. 2009). Symptoms of ZC include an internal

Published online: 13 December 2013

brown discoloration in potato tubers and striped and streaky appearance when the tubers are fried (Hansen et al. 2008; Munyaneza et al. 2009; Munyaneza 2010). This disease results in millions of dollars in losses to the potato industry in the United States (Munyaneza et al. 2007a, b, 2009) and yield losses that can exceed 80 % (Munyaneza et al. 2008). Currently, the control of *B. cockerelli* and the bacterial disease this insect transmits (ZC complex) depends on the use of chemical insecticides (Liu and Trumble 2005; Goolsby et al. 2007; Gharalari et al. 2009).

Chemical control is expensive, can reduce populations of natural enemies, and has led to the development of resistance (Liu and Trumble 2007). Therefore, it is important to find alternative methods for control, such as host plant resistance, which can be the foundation of an integrated pest management (IPM) program (Panda and Khush 1995; Kennedy 2008). Moreover, the use of resistant cultivars may offer a long-term solution for controlling *B. cockerelli* and the bacterial pathogen, leading to reduced application of insecticides. Butler et al. (2011) studied the behavior of *B. cockerelli* adults on 22 potato genotypes and found differences in the occurrence and duration of probing, duration of cleaning and resting, time spent off the potato leaves and the transmission of the bacterial pathogen, *Candidatus* Liberibacter psyllaurous. These behavioral differences of *B. cockerelli* among different genotypes seem to indicate the presence of antibiosis, plant characteristics that adversely affect the biology of the insect (Smith 2005) and mainly antixenosis, plant characteristics that drives insects away from the host (the plant is a poor host to the insect) (Smith 2005). Antixenosis can play an important role in the control of the bacterial pathogen because *B. cockerelli* adults may avoid colonization of the resistant plants, which can significantly reduce the transmission of *Candidatus* Liberibacter psyllaurous.

Therefore, this study was conducted with the objective to characterize the categories of resistance of selected potato genotypes to *B. cockerelli* by conducting no-choice tests to identify antibiosis, and choice tests to identify antixenosis (or nonpreference).

Materials and Methods

Insect Culture and Plant Material Bactericera cockerelli populations used in these experiments were originally collected from tomato fields in Weslaco (Hidalgo County, Texas, USA) in June 2005 and were maintained on tomato 'Yellow Pear' plants under greenhouse conditions at 20–30 °C and 20–40 % RH, with a photoperiod of 14:10 (L:D) h at the University of California, Riverside, Department of Agricultural Operations. Tomato plants were grown in plastic pots (10.0 cm in diameter by 10.0 cm in height) with one plant per pot, and replaced as necessary. A total of five potato genotypes were used in this study, which included four genotypes ('A05379-211', 'NY138', 'P2-4' and 'TX05249-10W') that were identified as resistant to the potato psyllid in previous studies (Butler et al. 2011) where behavior of *B. cockerelli* adults on these genotypes was significantly affected compared to susceptible varieties. Furthermore, the genotypes 'TX05249-10W' and 'NY138' were also screened in the field by the Texas Potato Breeding and Variety Development Program and found to be putatively tolerant to the ZC complex (Butler et al. 2011). The potato variety 'Atlantic' was used as a susceptible check. The characterization of the breeding clones used in this study was previously reported by Novy and Helgeson (1994) and Butler et al. (2011). Potato genotypes used in all the experiments were grown from tubers (under greenhouse conditions mentioned above) in plastic pots (15 cm in diameter by 25 cm in height) with UC mix (Matkin and Chandler 1957) and fertilized three times per week with the label rate of Miracle Gro nutrient solution (Scotts Company, Marysville, OH, USA).

Choice Test (Antixenosis) The plants were planted individually in plastic pots (15 cm in diameter by 25 cm in height). Six weeks later, five pots (each containing one of the genotypes) were placed inside a rearing and observation cage (1466C, BioQuip, Rancho Dominguez, CA; 96 cm in length by 56 cm in width by 56 cm in height). Plants in the cage were randomized and there were five replications. A total of 60 similar-aged female psyllid adults were released at the center of the pots. The number of adults and eggs laid on each plant was counted 24 h later.

No-Choice Test (Antibiosis) For this experiment, the plants were planted individually in plastic pots (15 cm in diameter by 25 cm in height). Six weeks later, two plants per genotype were selected and each plant was infested with similar-aged potato psyllid adults; five males and five females were confined in a foam cage (7 cm in length by 6 cm in width by 1.5 cm in height) with a 7 cm^2 (3.5 cm in length by 2 cm in

Table 1 Free-choice antixenosis test: number of *B. cockerelli* adults and eggs per plant found on different potato genotypes after 24 h of releasing 60 female adults per replicate

Genotype	Adults (mean ± SEM)[a]	Eggs (mean ± SEM)[a]
Atlantic	13.4±1.9a	114.4±11.2a
NY 138	10.8±2.6a	62.0±17.9a
TX 05249-10W	10.0±3.0a	76.0±20.0a
P2–4	9.8±1.8a	55.8±12.7a
A05379-211	10.4±3.7a	79.2±18.3a

[a] Average of 5 replicates, 60 female adults per replicate

Within a column, means followed by different letters are significantly different ($P< 0.05$; Tukey's test)

Table 2 No-choice antibiosis test: total number of *B. cockerelli* eggs, nymphs and adults per plant produced by five male and five female confined adults for 4 h on different potato genotypes and percentage of survivorship from eggs to adults

Genotype	Eggs (mean ± SEM)[a]	N1 (mean ± SEM)[b]	N2 (mean ± SEM)[b]	N3 (mean ± SEM)[b]	N4 (mean ± SEM)[b]	N5 (mean ± SEM)[b]	Adults (mean ± SEM)[b]	Survivorship (mean ± SEM)[b]
Atlantic	30.1±4.5a	23.5±4.0a	21.9±3.4a	19.5±2.9a	18.8±2.7a	17.8±2.4a	16.8±2.0a	58.0±3.9a
NY 138	24.8±3.3a	15.3±2.0a	12.5±1.8a	11.3±2.0a	10.5±2.0a	9.0±1.9b	7.6±1.7b	31.0±5.8c
TX 05249-10W	27.0±3.1a	21.1±2.9a	18.8±2.9a	14.6±2.0a	12.8±1.8a	11.0±1.3b	10.8±1.1b	42.5±4.7bc
P2–4	27.1±3.6a	20.9±2.4a	16.4±2.7a	13.1±2.9a	10.9±2.2a	8.4±1.8b	7.3±1.6b	28.7±6.1c
A05379-211	24.3±3.9a	18.3±2.8a	17.1±2.7a	16.6±2.7a	14.5±2.1a	13.3±1.7ab	12.0±1.7b	51.5±3.6ab

[a] Average of 8 replicates, eggs produced by five male and five female confined adults for 4 h

[b] Average of 8 replicates

Within a column, means followed by different letters are significantly different ($P< 0.05$; Tukey's test)

width) rectangular hole. There were four cages per plant (fixed to the upper side of leaves) for a total of eight replications per genotype, representing a total of 80 psyllids (40 males and 40 females) per each genotype evaluated. The five female adults in each cage were allowed to lay eggs for 4 h after confinement, after which all cages and adults were removed and eggs were counted.

The plants (containing eggs) were moved to a room (25–30 °C and 40 % RH, with supplemental lights set for a period of 14:10 [L:D] h) and arranged in a completely randomized design. The developmental time (days) spent by *B. cockerelli* in each stage (eggs and nymphal instars 1 to 5) was recorded. Daily counts were also made to record the number of individuals (nymphal instars 1 to 5 and adults). Development time and counts of individuals were made daily until the last adult emerged. And *B. cockerelli* survivorship from eggs to adults was calculated on each genotype.

Statistical Analyses For the antibiosis and antixenosis tests, analysis of variance (ANOVA) for *B. cockerelli* populations among potato genotypes was conducted by using PROC GLM (SAS Institute 2003). Post hoc multiple comparisons were computed by using Tukey's studentized range test ($P< 0.05$) (SAS Institute 2003). The variables for the analysis were genotypes, number of adults and eggs; and genotypes, number of nymphs, number of adults and development time (days) for the antixenosis and antibiosis experiments, respectively. For the antibiosis experiment, the cages within a plant were strategically distributed to avoid interference of insects after the cages were removed and through the length of the experiment. Then, we used each cage as a repetition.

Results

Antixenosis There were no significant differences in the number of adults found after 24 h of releasing female psyllid adults ($F= 0.23$; df=4, 16; $P= 0.915$) or the number of eggs that females laid ($F= 1.73$; df=4, 16; $P< 0.193$) during that period among the five genotypes (Table 1).

Antibiosis The average number of eggs laid by five females after 4 h of confinement did not differ among the genotypes ($F= 0.36$; df=4, 28; $P= 0.835$) (Table 2). There were no significant differences in the number of first (N1) ($F= 1.06$; df=4, 28; $P= 0.397$), second (N2) ($F= 1.54$; df=4, 28; $P=0.217$), third (N3) ($F= 1.59$; df=4, 28; $P=0.204$) and

Table 3 No-choice test: developmental (days) of *B. cockerelli* eggs and nymphs on different potato genotypes and total developmental time (days) N1 to adults

Genotype	Eggs (mean ± SEM)[a]	N1 (mean ± SEM)[a]	N2 (mean ± SEM)[a]	N3 (mean ± SEM)[a]	N4 (mean ± SEM)[a]	N5 (mean ± SEM)[a]	Total (N1-N5)[a]
Atlantic	10.1±0.3a	4.4±0.3a	3.9±0.4a	4.0±0.3a	5.9±0.7a	8.5±0.4a	26.6±1.5a
NY 138	10.3±0.4a	4.5±0.2a	3.8±0.3a	5.1±0.6a	6.1±0.5a	9.6±1.4a	29.1±1.8a
TX 05249-10W	9.3±0.5a	4.9±0.4a	5.6±0.7a	6.4±0.9a	7.3±0.6a	10.4±0.5a	34.5±2.2a
P2–4	9.6±0.7a	4.8±0.3a	5.3±0.5a	5.5±0.8a	7.0±0.8a	10.3±1.2a	32.8±2.3a
A05379-211	9.8±0.6a	4.4±0.4a	4.4±0.4a	5.8±0.8a	6.6±1.0a	11.9±0.9a	33.0±2.7a

[a] Average of 8 replicates

Within a column, means followed by different letters are significantly different ($P< 0.05$; Tukey's test) fourth (N4) (F= 2.46; df=4, 28; P= 0.07) instars among the five genotypes (Table 2). The number of fifth (N5) instars (F= 4.46; df=4, 28; P= 0.007) and the survivorship from eggs to adults (F= 6.95; df=4, 28; P< 0.001) were significantly greater in the susceptible genotype compared to the resistant genotypes except for 'A05379-11' (Table 2). There were significantly (F= 5.95; df=4, 28; P< 0.001) fewer adults that developed from eggs on all resistant genotypes compared to the susceptible genotype 'Atlantic' (Table 2).

There were no significant differences in the number of developmental days that *B. cockerelli* eggs (F= 0.62; df=4, 28; P= 0.654), first (N1) (F= 0.74; df=4, 28; P= 0.571), second (N2) (F= 3.89; df=4, 28; P=0.012), third (N3) (F= 1.86; df=4, 28; P=0.146), fourth (N4) (F= 0.64; df=4, 28; P= 0.640) and fifth (N5) (F= 1.59; df=4, 28; P= 0.206) instars required among the five genotypes (Table 3). There were no significant differences in the total development time from N1 to adults (F= 2.51; df=4, 28; P= 0.064) among the genotypes (Table 3).

Discussion

The results from the no-choice experiments indicate a strong antibiotic effect of all four resistant genotypes evaluated against *B. cockerelli*; ca. 1.4 to 2.3-fold more adults developed from eggs on the susceptible genotype compared to resistant genotypes. Moreover, the number of fifth instars was higher on the susceptible genotype compared with most of the resistant genotypes evaluated. And the survivorship of *B. cockerelli* on the susceptible check was ca. 15 and 29 % higher compared with three of the resistant genotypes. Interestingly, the results of Butler et al. (2011) indicate that these same genotypes may also possess antixenosis as a category of resistance to *B. cockerelli*, because they found significant differences in the duration of behaviors such as cleaning ('A05379-211', 'NY138', 'P2-4' and 'TX05249-10W'), probing ('A05379-211', 'NY138', and 'TX05249-10W'), resting ('NY138' and 'TX05249-10W') and time spent off potato leaf ('A05379-211' and 'NY138') compared with susceptible genotypes. However, sometimes it is not straightforward to separate the effect of antibiosis from antixenosis on insect development (Panda and Khush 1995; Smith 2005). For example, in this study the strong antibiosis found in all the resistant genotypes in the no-choice test could have been derived from an antixenotic effect due to a reduction in feeding by *B. cockerelli* on the resistant genotypes throughout their development time or to adverse effects on the biology of *B. cockerelli* caused by feeding on the resistant genotypes. It seems that the reduced numbers of adults developing on the resistant genotypes compared to the susceptible 'Atlantic' were due to genetic characteristics that increased developmental times or increased nymph mortality through time. Additional research will be necessary to document if the observed resistance was due to plant defensive chemistry, physical defenses, or some other factor.

Although, there were no significant differences in the development time of *B. cockerelli* among all the genotypes; the insects on the genotype 'TX05249-10W' required the longest development time compared to insects on the other cultivars and development of *B. cockerelli* on this genotype took ca. 8 d more than on the susceptible genotype; and, the numbers of adults developing from eggs in the four resistant genotypes were statistically reduced compared to the susceptible genotype 'Atlantic'. This indicates that *B. cockerelli* on resistant genotypes have statistically the same developmental time as the susceptible check, yet the number of *B. cockerelli* reaching adulthood is significantly lower for all the resistant genotypes compared to the susceptible cultivar.

In this research, we used simple methodology to study potato resistance to *B. cockerelli*. Furthermore, we found a strong antibiotic effect in all the resistant genotypes to *B. cockerelli*. Therefore, we recommend that future studies focus on studying the specific genetic traits of these potato genotypes that confer resistance to *B. cockerelli* in order to incorporate resistant genes into commercial potato varieties. Further research is needed to address this question. It might be also useful to combine host plant resistance with other approaches such as the use of repellents. Diaz-Montano and Trumble (2013) investigated the behavioral response of *B. cockerelli* to several potential repellents using a Y-tube olfactometer assay. Their results indicated that Dimethyl Disulfide (DMDS) and the oils of thyme, tea tree, peppermint, savory and clove were all highly repellent to *B. cockerelli*. This research shows there is potential for incorporation of resistant genotypes into an IPM program against *B. cockerelli*.

Acknowledgments We thank Bill Carson, Greg Kund, Deborah De La Riva, Kristen Hladun, Christina Mogren, Sammuel Gilbert, Khoa Tran (Chris), Kristine Gilbert and Lindsay Johnson for helping in different aspects of this study. This research was partially funded by a USDA SCRI grant (2009-34381-20036), a USDA RAMP grant (2009-51101-05892) and the California Potato Board. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture, Texas A & M University or the University of California-Riverside. USDA is an equal opportunity provider and employer.

References

Al-Jabr, A.M., and S.C. Whitney. 2007. Trapping tomato psyllid, Bactericera cockerelli (Sulc) (Hemiptera: Psyllidae), in greenhouses. *Southwestern Entomologist* 32: 25–30.

Butler, C.D., and J.T. Trumble. 2012. The potato psyllid Bactericera cockerelli (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies. *Terrestrial Arthropod Reviews* 5: 87–111.

Butler, C.D., B. Gonzalez, K.L. Manjunath, R.F. Lee, R.G. Novy, J.C. Miller, and J.T. Trumble. 2011. Behavioral responses of adult potato psyllid, Bactericera cockerelli (Hemiptera: Triozidae), to potato germplasm and transmission of Candidatus Liberibacter psyllaurous. *Crop Protection* 30: 1233–1238.

Diaz-Montano, J., and J. Trumble. 2013. Behavioral responses of the potato psyllid (Hemiptera: Triozidae) to volatiles from dimethyl disulfide and plant essential oils. *Journal of Insect Behavior* 26: 336–351.

Gharalari, A.H., C. Nansen, D.S. Lawson, J. Gilley, J.E. Munyaneza, and K. Vaughn. 2009. Knockdown, mortality, repellency, and residual effects of insecticides for control of Bactericera cockerelli adult (Hemiptera: Psyllidae). *Journal of Economic Entomology* 102: 1032–1038.

Goolsby, J.A., J. Adamczyk, B. Bextine, D. Lin, J.E. Munyaneza, and G. Bester. 2007. Development of an IPM program for management of the potato psyllid to reduce incidence of zebra chip disorder in potatoes. *Subtropical Plant Science* 59: 85–94.

Hansen, A.K., J.T. Trumble, R. Stouthamer, and T.D. Paine. 2008. A new Huanglongbing species, "Candidatus Liberibacter psyllaurous", found to infect tomato and potato, is vectored by the psyllid Bactericerca cockerelli (Sulc). *Applied and Environmental Microbiology* 74: 5862–5865.

Kennedy, G.G. 2008. Integration of insect-resistant genetically modified crops within IPM programs. In *Integration of insect-resistant genetically modified crops within IPM programs*, ed. J. Romeis, A.M. Shelton, and G.G. Kennedy, 1–26. Amsterdam: Springer.

Liefting, L.W., X.C. Perez-Egusquiza, and G.R.G. Clover. 2008. A new 'Candidatus Liberibacter' species in Solanum tuberosum in New Zealand. *Plant Disease* 92: 1474.

Liefting, L.W., P.W. Southerland, L.I. Ward, K.L. Paice, B.S. Weir, and G.R.G. Clover. 2009. A new "Candidatus Liberibacter" species associated with diseases of solanaceous crops. *Plant Disease* 93: 208–214.

Liu, D.G., and J.T. Trumble. 2005. Interactions of plant resistance and insecticides on the development and survival of Bactericerca cockerelli [Sulc] (Homoptera: Psyllidae). *Crop Protection* 24: 111–117.

Liu, D.G., and J.T. Trumble. 2006. Ovipositional preferences, damage thresholds, and detection of the tomato-potato psyllid Bactericera cockerelli (Homoptera: Psyllidae) on selected tomato accessions. *Bulletin of Entomological Research* 96: 197–204.

Liu, D.G., and J.T. Trumble. 2007. Comparative fitness of invasive and native populations of the potato psyllid Bactericerca cockerelli. *Entomologia Experimentalis et Applicata* 123: 35–42.

Matkin, O.A., and P.A. Chandler. 1957. The U.C.-type soil mixes. In *The U.C. system for producing healthy container-grown plants through the use of clean soil, clean stock and sanitation*, ed. K. Baker, 68–85. Berkeley: California Agricultural Experiment Station Manual 23.

Munyaneza, J.E. 2010. Psyllids as vectors of emerging bacterial diseases of annual crops. *Southwestern Entomologist* 35: 471–477.

Munyaneza, J.E., J.M. Crosslin, and E.J. Upton. 2007a. Association of Bactericera cockerelli (Homoptera: Psyllidae) with "Zebra Chip", a new potato disease in Southwestern United States and Mexico. *Journal of Economic Entomology* 100: 656–663.

Munyaneza, J.E., J.A. Goolsby, J.M. Crosslin, and E.J. Upton. 2007b. Further evidence that Zebra Chip potato disease in the Lower Rio Grande Valley of Texas is associated with Bactericera cockerelli. *Subtropical Plant Science* 59: 30–37.

Munyaneza, J.E., J.L. Buchman, J.E. Upton, J.A. Goolsby, J.M. Crosslin, G. Bester, G.P. Miles, and V.G. Sengoda. 2008. Impact of different potato psyllid populations on Zebra Chip disease incidence, severity, and potato yield. *Subtropical Plant Science* 60: 27–37.

Munyaneza, J.E., V.G. Sengoda, J.M. Crosslin, G. de la Rosa-Lozano, and A. Sanchez. 2009. First report of Candidatus Liberibacter psyllaurous in potato tubers with Zebra Chip disease in Mexico. *Plant Disease* 93: 552.

Novy, R.G., and J.P. Helgeson. 1994. Somatic hybrids between Solanum etuberosum and diploid, tuber bearing Solanum clones. *Theoretical and Applied Genetics* 89: 775–782.

Panda, N., and G.S. Khush. 1995. *Host plant resistance to insects*. Wallingford: CAB International.

SAS Institute. 2003. *SAS/STAT user's guide, version 9.1.3*. Cary: SAS Institute.

Smith, C.M. 2005. *Plant resistance to arthropods: molecular and conventional approaches*. Amsterdam: Springer.

Teulon, D.A.J., P.J. Workman, K.L. Thomas, and M.C. Nielsen. 2009. Bactericera cockerelli: incursion, dispersal and current distribution on vegetable crops in New Zealand. *New Zealand Plant Protection* 62: 136–144.