Insect Molecular Biology

Insect Molecular Biology (2013) **22**(1), 12–17 doi: 10.1111/j.1365-2583.2012.01165.x

Genome size and ploidy of Thysanoptera

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Abstract

Flow cytometry was used to study the genome sizes and ploidy levels for four thrips species: *Frankliniothrips orizabensis* Johansen (Thysanoptera: Aeolothripidae), *Frankliniella occidentalis* Pergande, *Frankliniella fusca* Hinds, and *Thrips tabaci* Lindeman (Thysanoptera: Thripidae). *F. orizabensis* males and females had 1C genome sizes of 426 Mb and 422 Mb, respectively. Male and female *F. fusca* had 1C genome sizes of 392 Mb and 409 Mb, whereas *F. occidentalis* males and females had smaller 1C genomes that were 345 Mb and 337 Mb, respectively. Male *F. orizabensis*, *F. occidentalis* and *F. fusca* were haploid and females diploid. Five isofemale lines of *T. tabaci*, initiated from parthenogenetic, thelytokous females and collected from different locations in North Carolina, were included in this study; no males were available. One isofemale line was diploid with a genome size of 1C = 310 Mb, and the other four had a mean genome size of 1C = 482 Mb, which is consistent with evidence from microsatellite data of diploidy and polyploidy, respectively, in these same five thelytokous lines. This is the first study to produce genome size estimates for thysanopteran species, and report polyploidy in *T. tabaci* populations.

First published online 4 November 2012.

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Keywords: Thysanoptera, genome size, polyploidy, flow cytometry.

Introduction

The insect order Thysanoptera, which comprises ~7400 species of thrips characterized by their small size (adults are 0.5–3 mm long) and the presence of fringe cilia on their wings, is composed of two suborders, Tubulifera and Terebrantia, containing one and eight families, respectively (Mound, 2005). Within the Thysanoptera, the most common mode of reproduction is through a haplodiploid sex-determination system, where males are haploid and derived from unfertilized eggs through arrhenotokous parthenogenesis, and females are diploid and produced biparentally (Moritz, 1997). In addition, thelytokous populations comprising only females produced parthenogenetically from unfertilized eggs, and deuterotokous populations in which both males and females are produced parthenogenetically are also known to occur (Moritz, 1997). Several species are reported to feed on fungus and pollen, or are predacious on other thrips and small arthropods (Milne & Walter, 1997, 1998; Agrawal *et al.*, 1999), while others are ectoparasites (Izzo *et al.*, 2002). In Australia, 21 tubuliferan species induce gall production on *Acacia* trees, and six of these species are eusocial with a morphologically distinct soldier caste, making them the only group of insects other than Hymenoptera that exhibit both haplodiploidy and eusociality (Crespi, 1992; Crespi & Mound, 1997; Kranz *et al.*, 1999). The majority of thrips are phytophagous (plant feeding) and include many economically important pests of agricultural crops (Lewis, 1997). In Terebrantia, 10 species in the family Thripidae are the sole vectors of plant-infecting tospoviruses that cause annual losses of over US$1 billion worldwide (Prins & Goldbach, 1998; Whitfield *et al.*, 2005; Pappu *et al.*, 2009).

The range of diversity exhibited by thrips and their economic impact on global agriculture mean they are excellent targets for genome sequencing efforts. Complete sequences of these insects will improve our understanding of specific traits of economic importance, and contribute to large-scale comparative studies across taxa. Genome size determination for candidate species is an

important first step used to inform sequencing efforts, and is valuable for the study of genome evolution, phylogenetics, cytogenetics and speciation, both within Insecta and across the tree of life (Gregory, 2005; Kraaijeveld, 2010; Loxdale, 2010). To date, of the ~1 000 000 described insect species (Grimaldi & Engel, 2005), genome size estimates are available for <1000 insect species (Hanrahan & Johnston, 2011). From these estimates, genome size trends in relation to metamorphosis have emerged. Holometabolous insects, those that undergo distinct egg, larval, pupal and adult life stages, exhibit constrained genome sizes that rarely exceed 2000 Mb, whereas, hemimetabolous insects, which have immature life stages similar in appearance to the adult, exhibit genome sizes that range from 105 to 15 980 Mb (Gregory, 2002; Hanrahan & Johnston, 2011). In addition to the necessity of additional genome size estimates for sequencing efforts, increasing the number of genome size estimates available for insects and other taxonomic groups across the tree of life provides additional information resources to advance the field of evolutionary genomics.

To date, no genome size estimates are available for any thysanopteran species (Hanrahan & Johnston, 2011; Gregory, 2012). The present study represents an initial step towards generating genome size and ploidy information for members of Thysanoptera. *Franklinothrips orizabensis* Johansen is a generalist predator and an important natural enemy in Californian avocado orchards (Hoddle, 2003). The other three thrips species selected for the present study, *Frankliniella occidentalis* Pergande, *Frankliniella fusca* Hinds and *Thrips tabaci* Lindeman, are important pests of many field and greenhouse crops worldwide, are three of the 10 reported vectors of tospoviruses, and are species targeted for sequencing efforts as part of a global effort to study virus transmission and insecticide resistance (Chiel *et al*., 2007; Rotenberg & Whitfield, 2010). In addition, observations of more than two alleles occurring at codominant microsatellite loci during development of population genetic markers have suggested the possibility that some populations of *T. tabaci* are polyploid (Jacobson and Booth, unpubl. data). In an initial screening of 12 microsatellite loci in 40 *T. tabaci* individuals collected from North Carolina, more than two alleles per locus were consistently seen in multiple individuals at multiple loci. Polyploidy has not been documented for any thrips species; however, Bournier (1956) suspected that *Heliothrips haemorrhoidalis* Bouché (Terebrantia, Thripidae) was triploid because this species has 21 chromosomes.

The specific objectives of the present study were to (1) determine the genome size of *F. orizabensis*, *F. occidentalis*, *F. fusca* and *T. tabaci*; (2) confirm haplodiploidy in *F. orizabensis*, *F. occidentalis* and *F. fusca* males and females; and (3) determine ploidy levels of *T. tabaci* isofemale lines exhibiting multiple alleles in single individuals.

Results and discussion

The genome size estimates for the three thrips species and their associated ploidy levels are given in Table 1. Two representative flow cytometry histograms from *T. tabaci* runs that show genome size determinations based on the relative fluorescence of samples compared with standards, and the detection of peaks that assist with ploidy determination are shown in Fig. 1. The mean genome size of 1C = 413.9 Mb (female) and 389.8 Mb (male) observed in the present study contrasts starkly with the that for hemimetabolous insects, 1C = 3205 Mb (Hanrahan & Johnston, 2011); however, it fits within the range for Insecta, 105–15 980 Mb, for closely related Phthiraptera (lice), and for distantly related Orthoptera [crickets and grasshoppers (Hanrahan & Johnston, 2011)]. Diploid *T. tabaci* had the smallest genome size estimate (1C = 310.6 Mb), followed by *F. occidentalis* (1C = 341.2 Mb), *F. fusca* (1C = 400.7 Mb), *F. orizabensis* (1C = 424.5 Mb), and polyploid *T. tabaci* (1C = 482.8 Mb). Male *F. orizabensis*, *F. occidentalis* and *F. fusca* were

Table 1. Flow cytometry genome size estimates and ploidy determination for three thrips species

Species	Sex	*n*	Mean 1C genome size (Mb)	SE (Mb)	Ploidy level	Maximum no. of alleles*
Franklinothrips orizabensis	F	4	426.2	7.6	Diploid	–
	M	4	422.8	14.9	Haploid	–
Frankliniella occidentalis	F	5	345	5.0	Diploid	–
	M	5	337.4	4.3	Haploid	–
Frankliniella fusca	F	6	392.1	2.0	Diploid	–
	M	1	409.2	–	Haploid	–
Thrips tabaci – Iso-1	F	2	491.3	7.8	Polyploid	3
Thrips tabaci – Iso-2	F	3	498.8	3.0	Polyploid	3
Thrips tabaci – Iso-3	F	8	482.9	26.8	Polyploid	3
Thrips tabaci – Iso-4	F	2	458.1	26.4	Polyploid	3
Average *T. tabaci* polyploid		15	482.8	16.5		
Thrips tabaci – Iso-5	F	3	310.6	9.4	Diploid	2

*The maximum number of alleles per locus observed at seven microsatellite loci.

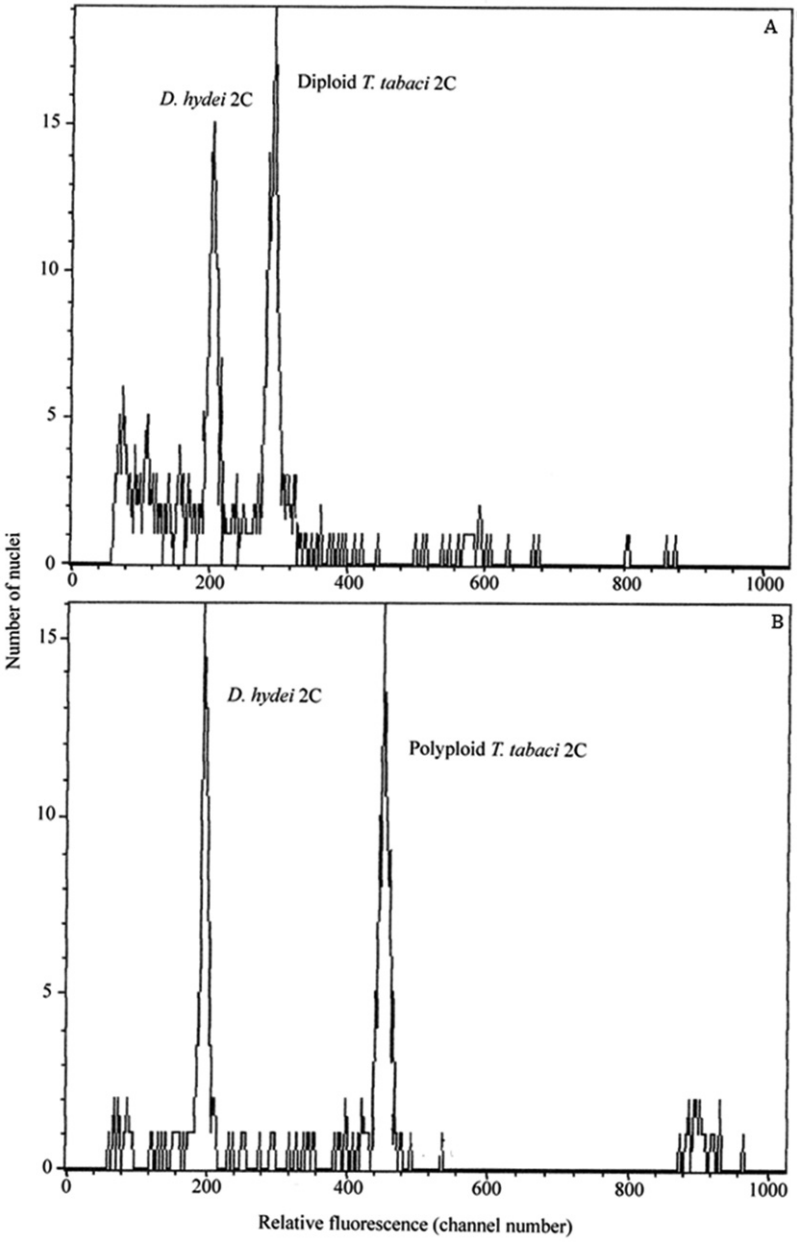

Figure 1. Flow cytometry histogram showing the relative fluorescence of co-prepared 2C nuclei from female *Drosophila hydei* nuclei and female diploid (A) and polyploid (B) *Thrips tabaci*. The genome size of *T. tabaci* is calculated as the ratio of the mean fluorescence of the 2C *T. tabaci* to the mean fluorescence of the 2C *D. hydei* nuclei times the amount of DNA in the latter (208 Mb). A small peak of 4C nuclei at fluorescence channel 900 (B) illustrates the important point that most nuclei from the head of both the sample and standard are 2C.

haploid with half the DNA amount per nucleus of that in a conspecific female diploid. Thrips genome size estimates are similar to the average genome size of Aphididae [aphids; 506 Mb (Gregory, 2012)], which represent the smallest in the order Hemiptera (true bugs, hoppers, cicadas, aphids) and are believed to be a sister group to Thysanoptera (Grimaldi *et al.*, 2004).

Two genome size estimates were produced for *T. tabaci*, one for diploids and one for polyploids (Table 1, Fig. 1). Of the five *T. tabaci* isofemale lines examined for ploidy level, only the Iso-5 strain appeared to be diploid. The other *T. tabaci* isofemale lines had larger genomes that were almost all identical. It is to be expected that a genome-wide duplication event causing polyploidy would increase DNA amount in direct proportion to the ploidy level, e.g. 2X, 4X, 6X, 8X. Interestingly, the larger genomes were 1.6 times larger than the diploid, which would be between a triploid and a tetraploid. Genome size reductions following the formation of polyploidy lines have been well documented in plants, but have been little studied in the animal kingdom (Leitch & Bennett, 2004). In Insecta, relationships between ploidy level and genome size are only available for one species, *Bacillus atticus carius* Brunner (Phasmida: Phasmatidae), for which the ratio of the genome size between diploid and triploid lines is 1.5, which is consistent with a proportional increase in ploidy and genome size (Normark, 1996). Nonlinear relationships between ploidy level and DNA content, moreover, have been observed in amphibian

and fish species whose ploidy levels are often >4*n*, which suggests genome reductions may occur outside of the plant kingdom (Mable *et al*., 2011). It is possible, therefore, that several of the *T. tabaci* lines represent ancient tetraploid events that have undergone a genome reduction. Although genome size estimates could also reflect triploid values that are inflated as a result of measurement error, the agreement of genome size estimates among the four polyploid lines coupled with microsatellite marker data discussed in the following paragraph provides evidence of tetraploidy in this species. Triploidy is harder to produce and maintain because it can result in unbalanced gametes and disrupt sex determination systems. The only way to maintain triploidy is through asexual reproduction that does not include meiosis (apomixis), whereas tetraploidy can be maintained sexually or asexually (automixis or apomixis).

Genome size estimates alone are not sufficient evidence of polyploidy; therefore, flow cytometry results were compared with the microsatellite allele profiles for parthenogenetically produced sisters of the thelytokous individuals used in the flow cytometry analysis. The flow cytometry results of ploidy for *T. tabaci* are consistent with observations from microsatellite marker development. A maximum of three bands per individual were observed at seven microsatellite loci for each of the four polyploid isofemale lines (consistent with polyploidy), while a maximum of two bands per individual were observed at these same loci for the diploid isofemale line [consistent with diploidy (Table 1)]. The additional bands observed in isofemale lines were not considered to result from microsatellite stutter bands. In addition, preliminary data for 40 *T. tabaci* individuals collected in North Carolina at 12 microsatellite loci produced a maximum of two, three and four alleles per individual (Jacobson and Booth, unpubl. data). Although only thelytokous individuals were available for use in the flow cytometry study, both thelytokous and arrhenotokous individuals were included in the microsatellite analyses. A maximum of four alleles per locus were observed in individuals with both reproductive modes. Additional studies are needed to evaluate variation in genome size and ploidy in *T. tabaci* from different geographic areas as well as in arrhenotokous populations and males. Although uncommon, rare matings between parthenogenetic and sexual populations can occur, and where they do, breeding structure can influence the establishment and persistence of polyploid lines (Schneider *et al*., 2003; Crespo-López *et al*., 2007; Jakovlić & Gui, 2011). Nothing is known about the breeding structure of *T. tabaci* populations, the scale of gene flow, or whether or not gene flow occurs between individuals of different reproductive modes. Future genomic sequencing efforts and studies identifying the process of gamete formation in sexually and asexually reproducing *T. tabaci* populations will help to identify the nature and maintenance of genome duplication and reduction events in this species.

This is the first report of polyploidy in *T. tabaci*, and the first account of variation in ploidy level among thrips populations. Polyploidy in *T. tabaci* is especially interesting because of the large amount of inter- and intrapopulation variation already described for this species in relation to host plant races (Chatzivassiliou *et al*., 2002; Brunner *et al*., 2004), transmission of tomato spotted wilt tospovirus (Chatzivassiliou *et al*., 2002; Cabrera-La Rosa & Kennedy, 2007), insecticide resistance patterns (Shelton *et al*., 2003), and the existence of arrhenotokous, thelytokous, and deuterotokous parthenogenesis (Kendall & Capinera, 1990; Jenser *et al*., 2006; Nault *et al*., 2006). In the animal kingdom, polyploidy is commonly associated with parthenogenesis, and can serve as a mechanism for population isolation, drive evolutionary changes and species divergence, and has been used to explain geographic patterns of population variation and range expansion in other insect species (Lundmark & Saura, 2006; Ghiselli *et al*., 2007). The prevalence of polyploidy in *T. tabaci* in relation to reproductive mode and geographic range may provide additional insights into the evolutionary impact of polyploidy. The prevalence of polyploidy in Thysanoptera is unknown, but it is likely that other polyploid species exist, based on chromosome number, parthenogenetic reproduction, and because polyploidy is assumed to be rare and therefore has not been considered in thrips studies.

Other available information regarding genomic size variation among thysanopterans comes from cytological studies examining chromosome number and karyotypes for six Tubulifera species in the family Phlaeothripidae and 14 terebrantian species in the family Thripidae (Pomeyrol, 1929; Prussard-Radulesco, 1930; Bournier, 1956; Risler & Kempter, 1961; Brito *et al*., 2010). Distinct chromosomal differences were observed between Phlaeothripidae and Thripidae, with chromosome number being greater and chromosome size being smaller in the latter than the former. In addition, the reports of four distinct chromosome numbers for the species *H. haemorrhoidalis* (Terebrantia, Thripidae) (Pomeyrol, 1929; Prussard-Radulesco, 1930; Bournier, 1956), and identification of distinct karyotypes for *Gynaikothrips uzeli* Zimmerman [Tubulifera, Phlaeothripidae (Brito *et al*., 2010)] suggest the presence of species complexes for members of both suborders of Thysanoptera. Future evaluations of the genome size, organization and ploidy in Thysanoptera are likely to yield valuable information on the evolution and diversity of thrips, as well as provide important comparisons to address broader evolutionary questions regarding the evolution of reproductive behaviour, haplodiploidy, eusociality, virus transmission and invasion biology.

Experimental procedures

Insect samples

Adult *F. orizabensis* were collected from avocado orchards in southern California. Other adult male and female thrips used in the present study were obtained from laboratory colonies. Colonies of *F. fusca*, originally collected from peanut (*Arachis hypogaea* L.) at the Peanut Belt Research Station in Lewiston, NC, USA, and *F. occidentalis* collected in Hawaii were maintained on *Phaseolus vulgaris* L. bean pods in controlled environments at 24 °C with ~60% relative humidity and a photoperiod of 14:10 (light:dark). Isofemale lines of *T. tabaci* were established from individual females collected from the following locations and host plants in North Carolina in 2010: from rye [*Secale cereal* L. (Iso-1)] and wild onion [*Alliums* spp. (Iso-2)] at the NCSU Sandhills Research Station in Jackson Springs, NC; from onion (*Allium cepa* L.) in Candor, NC (Iso-3); from wild onion in Cove City, NC (Iso-4), and from onion at the NCSU Kinston Agricultural Research Station in Kinston, NC, USA (Iso-5). Reproduction in each of these isofemale lines was by thelytokous parthenogenesis, in which all female offspring are produced asexually, therefore, only female offspring were available for the present study. Colonies of *T. tabaci* were reared on cabbage (*Brassica oleracea* L.) in environmental chambers at 23 °C and a photoperiod of 14:10 (light:dark).

Flow cytometry

Genome size and ploidy levels were determined using flow cytometry of propidium iodide-stained nuclei according to Hare and Johnston 2011. Heads were dissected from thrips adults that had been flash frozen in liquid nitrogen. The heads were then placed in ice-cold Galbraith buffer, along with 1/10 of a head of a *Drosophila virilis* (1C = 328 Mb) for *F. fusca*, or *Drosophila hydei* (1C = 208 Mb) for *F. occidentalis*, *F. orizabensis* and *T. tabaci*, ground using a Kontes Dounce tissue grinder, and filtered through a 20-μm mesh. Nuclei were then stained with 25 μg/ml propidium iodide for 0.5 h. The mean fluorescence of stained nuclei was quantified using a Partec CyFlow with a solid-state laser emitting 532 nm. The position of the 2C sample peak relative to the 2C *D. virilis* standard was verified by running at least one insect of each species without a standard. To determine the total quantity of DNA in the sample, the ratio of the mean fluorescence of the 2C peak of the sample to the mean fluorescence of the 2C peak of the standard was calculated, and this ratio was multiplied by the 1C amount of DNA in the standard, where 1C refers to the mean amount of DNA in a haploid nucleus.

Acknowledgements

We would like to thank Mark Hoddle for providing the *F. orizabensis* used in this study, and the North Carolina Tobacco Research Commission for providing partial funding for this work.

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