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ORIGINAL ARTICLE

Efficiency of food utilization by *Dichroplus maculipennis* (Orthoptera: Acrididae: Melanoplinae) on four crop plants under controlled conditions

Y. Mariottini[a], C. E. Lange[b,c], R. Cepeda[a] and M. L. De Wysiecki[b,d]

[a]Instituto Multidisciplinario sobre Ecosistemas y Desarrollo Sustentable (UNICEN-CIC), Tandil, Argentina; [b]Centro de Estudios Parasitológicos y de Vectores (CONICET-UNLP), La Plata, Argentina; [c]Comisión de Investigaciones de la Provincia de Buenos Aires (CICPBA), La Plata, Argentina; [d]Facultad de Ciencias Naturales y Museo (UNLP), La Plata, Argentina

ABSTRACT

The aim of this study was to analyze the food utilization efficiencies and the relative growth and consumption rates of different developmental stages and sexes of *D. maculipennis* under controlled conditions on wheat, oat, corn, and soybean plants, important crops in the Pampas region of Argentina. As expected from a polyphagous species, *D. maculipennis* was observed to consume all four of the plant species offered. Nevertheless, the consumption of both nymphs and adults was differentiated. Oat and wheat were more consumed than corn and soybean. Females presented higher consumption rates (384.6 ± 30.64 mg/individual/day) than males (278.71 ± 24.26 mg/individual/day). Adult females had the highest growth rate, followed by nymphs of the same sex, and then adult males. The highest values of ECI and ECD were obtained in soybean; females had higher values of food efficiencies than males, and nymphs had greater values than adults. In relation to this, soybean was the highest quality food; the amount of nitrogen present in soybean was approximately twice that found in the other species. The nutritional needs of *D. maculipennis* might have been satisfied by feeding on low quantities of soybean, which is, among the food offered, the most "nutritionally balanced food".

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Grasshopper; nutritional efficiencies; Argentina; crops

Introduction

Grasshoppers are often dominant native herbivores in grassland ecosystems worldwide and play a key role as primary consumers, as components of the trophic network, and in the cycling of nutrients and energy of the ecosystem (Belovsky 2000; Branson et al. 2006). Some species of grasshoppers are considered pests and in years of outbreaks cause serious damage to both crops and rangeland and compete with cattle for forage (Fielding & Brusven 1995; Jonas & Joern 2008; Cigliano et al. 2014). In Argentina, the economic importance of these insects has been recognized since the mid to late nineteenth century due to the recurrent outbreaks of different species (Lange et al. 2005). Of the 204 grasshopper species known for the country, about 19 are considered pest species. Among them, one of the most serious is *Dichroplus maculipennis* (Blanchard 1851), mainly in areas of the Pampas and Patagonia regions, where it constitutes a major problem to several crops and natural pastures (COPR 1982; Carbonell et al. 2017). In the southern Pampas, *D. maculipennis* is normally found in natural grasslands, preferably of low grasses and halophilous soils. However, during outbreak situations and due to its high dispersal capacity, *D. maculipennis* usually invades crops (barley, rye, oat, wheat, flax, lucerne, corn) and pastures, causing significant damage (Figures 1 and 2) (Mariottini et al. 2012).

The pampas region of Argentina constitutes one of the most intensively- and extensively – used agricultural landscapes in South America. In the last decades, agriculture has expanded further and increased the replacement of natural grasslands by crops or annual pastures, homogenizing the landscape and fragmenting the native vegetation that constitutes the habitat of many species (Viglizzo et al. 2011). In parallel, productivity increased in response to the application of external inputs, modern technology, and management practices (Satorre 2005). This region contributes with more than 80% of the total national production of soybean, corn, and wheat (Rótolo et al. 2014). Oats is one of the most important winter cereals intended for cattle feeding in the country; in Buenos Aires province, it is found in 56% of the planted area (Moreyra et al. 2014).

The economic importance of *D. maculipennis* in the Pampas region is recognized historically, and to date, chemical insecticides are the only available option for

CONTACT Y. Mariottini ymariottini@cepave.edu.ar

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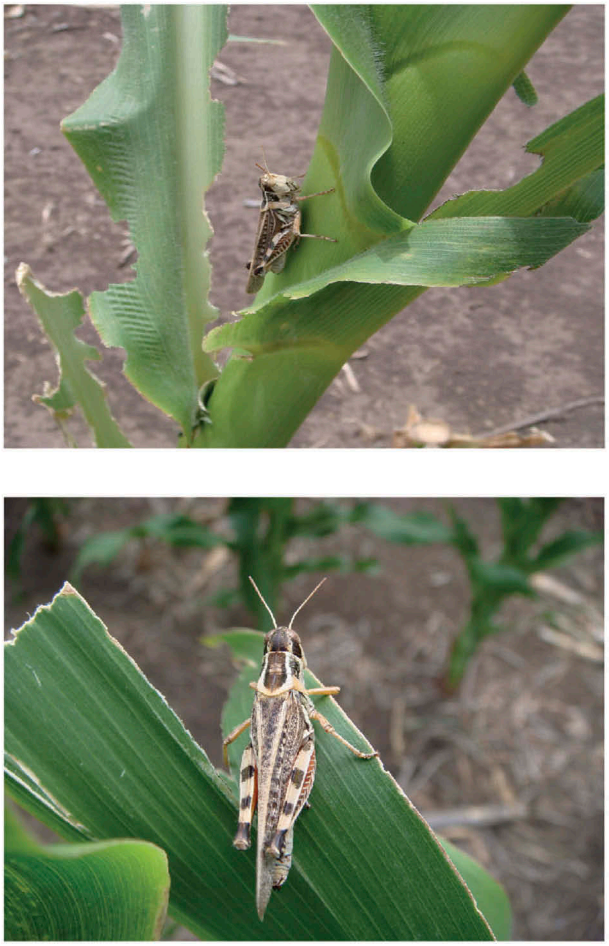

Figure 1. Individuals of *Dichroplus maculipennis* in corn plants, 2009 December, Buenos Aires province, Argentina.

grasshopper control, but the use of such chemical agents is of serious environmental concern (Gonzalez et al. 2010). Therefore, we consider that knowing and evaluating different aspects of the feeding behavior of a grasshopper species considered a pest is an important step when establishing plans for the rational management of these insects. In relation to this, the consumption of older nymphs and adults of *D. maculipennis* has been estimated in recent years under controlled conditions on *Bromus brevis*, a native Poaceae species of important forage value (Mariottini et al. 2011). In addition, the loss of forage caused by different densities of *D. maculipennis* in adulthood in a pasture of such forage value as *Festuca arundinacea* was evaluated under field conditions (Mariottini et al. 2018). On the other hand, Pelizza et al. (2017) examined the effects of the entomopathogenic fungi *Beauveria bassiana* as an endophyte in corn plants on consumption and food preference of adults of *D. maculipennis.*

In order to continue studying different aspects of the nutritional ecology of *D. maculipennis*, the aim of this study was to analyze the food utilization efficiencies and the relative growth rate and consumption rate on *Triticum aestivum* (wheat), *Avena sativa* (oat), *Zea mays* (corn) and *Glycine max* (soybean), four of the most economically important crops of the Pampas region.

Materials and methods

Experiments conducted in this study were performed with juveniles (6th instar nymphs) and adults of both sexes of *D. maculipennis*. These individuals belonged to the first laboratory generation (F1) of specimens originally collected in Laprida county (37° 32′ 60″ S, 60° 49′ 00″W), Buenos Aires province, Argentina. These developmental stages were selected because under laboratory conditions, Mariottini et al. (2011) registered that the older nymphs and pre-reproductive adults of *D. maculipennis* are the developmental stages that made the highest consumption.

Seeds of the different crop plant species used (*Triticum aestivum, Avena sativa, Zea mays* and *Glycine max*) were planted in 500 cm^3 plastic pots at a depth of 15 cm, filled with a sterile mixture of perlite, vermiculite, and ground in equal amounts. Plants were watered daily and were maintained in a greenhouse at 25°C and a 12–12 h light-darkness photophase (Pelliza

Figure 2. Individuals of *Dichroplus maculipennis* in soybean plants, 2009 December, Buenos Aires province, Argentina.

et al. 2017). The plants used in the experiments were between 20 and 25 days old. Only the leaf blades were used in the experiments (both, in the chemical analyses and those that were offered to insects), in order to reduce the effect of heterogeneity between plant parts, thus minimizing any effects of dietary selection action by the grasshoppers (Clissold 2003).

In order to know the nutritional quality of the plants, nitrogen, a structural and non-structural carbohydrate, analyses were carried out. Nitrogen analyses were performed at the Laboratory of Analytical Services of Soils, Plants and Environment (LABSPA), Centre of Renewable Natural Resources in Semi-arid Zones (CERZOS – CONICET), Bahía Blanca. Nitrogen content was estimated through semimicro-Kjeldahl methods (Nelson & Sommers 1973). Structural and non-structural carbohydrate analyses were performed at the Animal Nutrition Laboratory, Agronomy Department of 'Universidad Nacional del Sur', Bahía Blanca. Structural carbohydrate components, Neutral detergent fiber (NDF), acid detergent fiber (ADF) were estimated according to the procedure described by Van Soest et al. (1991). Non-structural carbohydrate components were estimated by the methods developed by Silva and Queiroz (2002). These parameters were evaluated on leaves of the plants that were cut at the same moment in which the consumption and other tests were carried out.

Relative consumption rate, relative growth rate, and food utilization efficiencies were estimated under controlled temperature (30ºC) and photophase: 14 light:10 darkness hours, conditions used in several studies (Yang & Joern 1994; Clissold et al. 2006; Mariottini et al. 2010; Pelliza et al. 2017). A total of 160 individuals were used, 40 individuals per stage of development and sex (i.e. 40 female nymphs, 40 male nymphs, 40 female adults and 40 male adults). The different parameters were evaluated in 10 individuals (according to sex and stage of development) per plant tested.

After 24 h of starvation, grasshoppers were weighed in a scale (accuracy of 10^{-4} g) and placed individually in a wire-screened, aluminum cage (12 × 12 × 16 cm) with a fresh ration of one of the four plant species utilized; 48 h later, grasshoppers, the remaining food, and feces were removed, oven-dried (at 60ºC to constant mass), and weighed (accuracy of 10^{-4} g). Ten control rations of each plant species were prepared and oven-dried *per* trial. Mean dry weight of control rations was used as a correction factor to calculate the dry weight of food offered to the grasshoppers. The difference in weight between the offered rations and the remaining material after a trial represented the consumption during the test (Clissold 2003; Mariottini et al. 2011; Franceschini et al. 2014).

The biomass gained *per* individual was calculated from the difference between initial and final dry weights. The initial dry weight of grasshoppers was derived from the fresh weight and a conversion factor, which was obtained by dividing the product of the dry weight/fresh weight of 10 grasshoppers of each sex and instar of development (Capello et al. 2011).

Rates of consumption, growth, and food utilization efficiencies, Efficiency of conversion of ingested food (ECI), Efficiency of conversion of digested food (ECD) and approximate digestibility (AD) were estimated following Raubenheimer and Simpson (1992) and Garcia-Garcia et al. (2008).

Data analyses

Water content and amounts of nitrogen and carbohydrates (structural and non-structural) of each plant species were compared through a one-way analysis of variance (ANOVA). The initial weight of grasshoppers was subjected to Kruskal Wallis Test. Nutritional indices and ecological efficiencies were analyzed by an analysis of covariance (ANCOVA) (Raubenheimer & Simpson 1992) with three factors (Plants species, sex, developmental stage). In order to estimate the relative rate of consumption, the ingested food was used as the dependent variable and the initial weight as its covariate. For relative rate of growth, the final weight was used as the dependent variable and the initial weight as its covariate; for ECI and ECD equivalent weight gained as the dependent variable was used, for ECI the ingested food was the covariate and the ingested food minus the fecal mass was the covariate used for ECD. Finally, for AD equivalent we used fecal mass as the dependent variable and ingested food as the covariate (Garcia-Garcia et al. 2008). All analyses were conducted with the InfoStat software (Di Renzo et al. 2014).

Results

The water content of each plant species was 86.8 ± 0.34% in oat, 88.46 ± 0.68 in corn, 86.24 ± 0.57% in soybean, and 93.10 ± 2.17% in wheat. There was no significant difference among them (Kruskal Wallis test, H = 5.38; P = 0.146). The nitrogen content registered in all four plant species was significantly different (ANOVA; F = 75.13; df = 3; $P < 0.0001$). The amount of nitrogen in soybean (4.62 ± 0.14%) was higher than that registered in the other plants. The lowest amount was recorded in oat (1.72 ± 0.10%) (Table 1). Regarding structural carbohydrates, differences were significant (ANOVA; F = 74.61; df = 3; $p < 0.0001$). The amount of structural carbohydrates recorded in corn (53.70 ± 1.15%) was higher than that observed in the other plants and was the lowest (37.34 ± 1.17%) in soybean. Finally, there were no significant differences between plants in terms of soluble or non-structural carbohydrate content (Kruskal Wallis test, H = 6.59; $p = 0.086$) (Table 1).

Average values *per* day of consumption, final weight reached, biomass gained, and amount of feces produced are presented according to sex and stage of development (Table 2).

Differences observed in the values of relative consumption rate were significant for plant species and sex factors, but not for development stage, as regards this, the nymphs (females and males) feed a mean of 157.20 ± 12.08 mg/individual/day and the adults (females and males) feed a mean of 177.18 ± 16.36 mg/individual/day (Table 3, Figure 3). Separating individuals by sex, the mean consumption per day of females (nymphs and adults) was 384.6 ± 30.64 mg/individual/day, significantly higher than that of males which was 278.71 ± 24.26 mg/individual/day (LSD Fisher $p < 0.05$). Oat and wheat were the two more consumed species, then corn, and finally soybean (LSD Fisher $p < 0.05$) (Figure 4). The interaction between plant species and sex factors was significant, the relative consumption rate of females was significantly higher in oat and wheat than in soybean and corn; also corn consumption was higher than soybean consumption (LSD Fisher, $p < 0.05$), both sexes consumed more oats and wheat than soybean and corn.

The initial weight of the grasshoppers was significantly different according to the stage of development and sex (Kruskal Wallis test, H = 75.47; $p < 0.0001$). Female adults were the heaviest (154.8 ± 5.04 mg), then male adults (97.82 ± 4.88 mg), female nymphs (61.66 ± 2.21 mg) and, finally male nymphs (45.17 ± 2.35 mg). Nevertheless, this variable used as covariate in the ANCOVA was not significant, suggesting that the initial weight does not influence the relative rate of consumption of the individuals (Table 3).

Results obtained from the growth rate analyses showed significant differences among the three factors, and the covariate 'initial weight' was significant (Table 3). Female adults had the highest growth rate, secondly the female nymphs, then the male adults and finally the male nymphs (LSD Fisher $p < 0.05$). The female adults had a similar growth rate feeding the four plant species offered (LSD Fisher $p > 0.05$) (Table 2). Nymphs of sexes and adult males that fed on soybean had a higher growth rate than those who fed on the other plants. The lowest growth rates were of the nymph males in corn and wheat (LSD Fisher $p < 0.05$).

The average final weight reached by the individual according to sex and stage of development after a day was: adult females 163.13 ± 5.21 mg, adult males 102.36 ± 5.26 mg, female nymphs 72.01 ± 2.46, male nymphs 52.81 ± 2.68. The interaction between plant species factor and developmental stage was significant. Adults had a similar rate of growth with the four species of plants, while nymphs that were fed with soybean had

Table 1. Mean content of nitrogen, structural and non-structural carbohydrates (±SE) in plants of oats, corn, wheat and soybean, expressed as percentage. In the columns, different letters indicate significant differences (LSD Fisher $p < 0.05$).

Plant species	Nitrogen	Structural carbohydrates	Non-structural carbohydrates
Oats	1.72 ± 0.10 d	50.39 ± 0.00 b	8.44 ± 0.91 a
Corn	2.30 ± 0.13 c	53.71 ± 1.55 a	5.28 ± 0.28 a
Wheat	3.04 ± 0.19 b	50.74 ± 0.36 b	6.66 ± 0.60 a
Soybean	4.62 ± 0.14 a	37.34 ± 1.17 c	5.02 ± 0.72 a

Table 2. Mean values (±SE) of relative consumption rate (mg/individual/day), final weight (mg), biomass gained (mg/day), and the amount of feces produced (mg) per day by *Dichroplus maculipennis* according to sex and stage of development. At laboratory conditions (30ºC, 14L:10D).

		Females		Males	
	Plant species	Nymphs	Adults	Nymphs	Adults
Relative consumption	Oats	267.32 ± 5.29	322.24 ± 45.50	210.05 ± 9.52	221.90 ± 19.09
	Wheat	229.33 ± 22.71	274.81 ± 39.31	174.41 ± 30.39	240.71 ± 20.97
	Corn	92.22 ± 5.21	222.41 ± 22.73	52.87 ± 3.94	64.37 ± 8.63
	Soybean	79.96 ± 12.20	78.11 ± 11.84	76.38 ± 18.28	71.54 ± 3.76
Final weight	Oats	65.67 ± 3.87	173.91 ± 20.53	50.05 ± 2.48	97.83 ± 11.84
	Wheat	74.21 ± 5.54	156.09 ± 3.68	43.47 ± 1.63	82.01 ± 12.84
	Corn	64.07 ± 6.05	169.05 ± 12.80	48.94 ± 1.46	107.77 ± 7.18
	Soybean	82.24 ± 1.23	158.00 ± 8.70	76.62 ± 1.23	121.18 ± 5.58
Biomass gained	Oats	10.86 ± 0.62	10.95 ± 1.16	8.35 ± 0.84	4.30 ± 1.78
	Wheat	8.23 ± 0.44	4.33 ± 0.94	6.15 ± 0.76	4.48 ± 1.40
	Corn	7.31 ± 1.61	7.89 ± 1.21	4.98 ± 0.84	4.36 ± 0.47
	Soybean	11.49 ± 1.31	12.13 ± 2.34	11.45 ± 0.95	8.27 ± 3.01
Faeces	Oats	57.48 ± 3.49	44.03 ± 3.88	44.30 ± 4.95	18.20 ± 5.18
	Wheat	62.13 ± 3.14	43.08 ± 2.10	36.75 ± 3.14	24.58 ± 4.28
	Corn	33.89 ± 6.86	43.08 ± 2.10	30.09 ± 1.96	28.39 ± 5.85
	Soybean	47.50 ± 4.41	60.70 ± 6.23	39.65 ± 7.27	34.73 ± 3.52

Table 3. Results of Covariance Analysis (ANCOVA) for the evaluation of relative consumption, relative growth, efficiency of conversion of ingested food (ECI), efficiency of conversion of digested food (ECD) and approximate digestibility (AD) in *Dichroplus maculipennis* at laboratory conditions (30ºC, 14L:10D).

Nutritional Indexes and food effiences			df	F	*p*-valor
Relative Consumption	Dependent variable	Ingested food			
	Model		16	17.38	<0.0001
	Factors	Plants	3	68.36	<0.0001
		Sex	1	6.50	0.0128
		Stage	1	0.03	0.857
	Covariate	Initial weight	1	2.24	0.138
	Interactions	Plants x Sex	3	3.04	0.033
		Plants x Stage	3	1.72	0.171
		Stage x Sex	1	0.45	0.510
		Plant x Stage x Sex	3	2.19	0.965
	error		75		
	total		91		
Relative Growth	Dependent variable	Final weight			
	Model		16	655.63	<0.0001
	Factors	Plants	3	7.64	0.0002
		Sex	1	25.59	<0.0001
		Stage	1	7.07	0,009
	Covariate	Initial weight	1	163.58	<0.0001
	Interactions	Plants x Sex	3	1.89	0.139
		Plants x Stage	3	2.95	0.038
		Stage x Sex	1	1.56	0.215
		Plant x Stage x Sex	3	1.87	0.143
	error		75		
	total		91		
ECI	Dependent variable	Biomass gained			
	Model		16	4.43	<0,0001
	Factors	Plants	3	9.61	<0.0001
		Sex	1	9.41	0,003
		Stage	1	9.32	0,003
	Covariate	Consumption	1	1.45	0,023
	Interactions	Plants x Sex	3	0.34	0.794
		Plants x Stage	3	2.26	0.088
		Stage x Sex	1	0.10	0.754
		Plant x Stage x Sex	3	2.71	0.055
	error		75		
	total		91		
ECD	Dependent variable	Biomass gained			
	Model		16	4.28	<0.0001
	Factors	Plants	3	8.54	0.0001
		Sex	1	7.14	0.009
		Stage	1	14.28	0.000
	Covariate	Consumption- Faeces	1	0.15	0.695
	Interactions	Plants x Sex	3	0.44	0.725
		Plants x Stage	3	2.18	0.098
		Stage x Sex	1	0.24	0.624
		Plant x Stage x Sex	3	2.89	0.061
	error		75		
	total		91		
AD	Dependent variable	Faeces amount			
	Model		16	6.06	<0.0001
	Factors	Plants	3	3.00	0.0361
		Sex	1	26.62	<0.0001
		Stage	1	6.58	0.0124
	Covariate	Consumption	1	1.10	0.2979
	Interactions	Plants x Sex	3	1.72	0.1708
		Plants x Stage	3	9.13	<0.0001
		Stage x Sex	1	3.84	0.054
		Plant x Stage x Sex	3	2.04	0.1160
	error		75		
	total		91		

a higher relative growth rate than those fed with the other plants. (LSD Fisher $p < 0.005$) (Figure 5).

Concerning the food efficiences estimated, in the ECI the three factors were significantly different but the covariate (consumption) was not significant (Table 3), indicating that consumption does not influence the ingestion efficiency. The ECI in soybean was the highest, followed by oat and then wheat and corn.

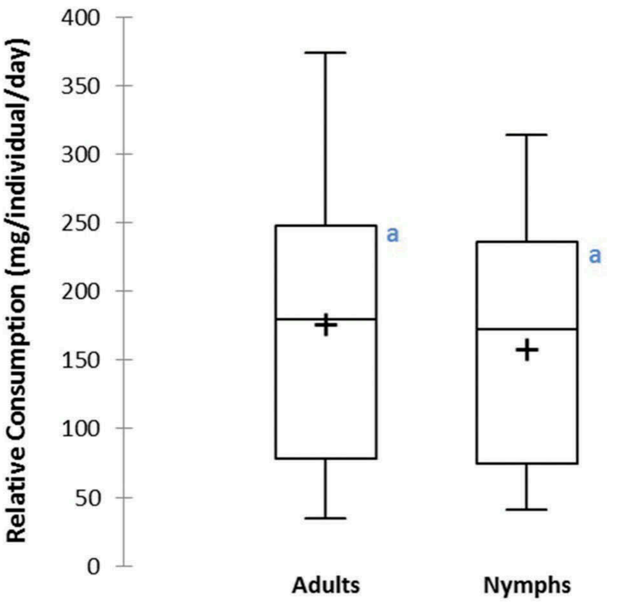

Figure 3. Relative consumption rate (mg/individual/day) of nymphs in 6th stage and adults of *Dichroplus maculipennis* at laboratory conditions (30ºC, 14L:10D). Different letters indicate significant differences (LSD Fisher p < 0.05).

Nymphs of both sexes had higher ECI than female and male adults; among the latter, the males had a lower ECI than the females. The highest ECI were of female nymphs feeding in soybean.

The results of the ANCOVA made for ECD the three factors were significantly different (LSD Fisher p < 0.0001) but not the covariate. The highest values of ECD, as ECI, were obtained in soybean and oat, then wheat and finally corn. The females had a higher ECD than males and individuals in nymphal stage greater than adults.

Regardless of sex and the state of development, the ECD was higher in individuals that were fed with soybean (10.75 mg/day) and oats (8.86 ± 0.67 mg/day) than those that were fed with corn and wheat (Figure 6). Nymphs had a greater ECD than adults; the biomass gained by nymphs (females and males) was 8.92 ± 0.48 mg/day and by adults (females and males) was 6.89 ± 0.73 mg/day (LSD Fisher p < 0.05). Finally, efficiencies were higher in females than in males, the mean biomass gained in females (nymphs and adults) was 9.46 ± 0.6 mg/day and in males 6.71 ± 0.6 mg/day (LSD Fisher p < 0.05).

With respect to the approximate digestibility, the three factors were significantly different (Table 3), but not the covariate (Consumption). The AD values in females were higher than in males (LSD fisher p < 0.0001), the amount of feces produced by females was 47.31 ± 7.21 mg/individual/day and for males 32.65 ± 4.61 mg/individual/day. The approximate digestibility was higher in nymphs than in adults, independently of sex the amount of faces produced by the nymphs was 42.30 ± 5.98 mg/individual/day, while the produced by adults was 36.08 ± 5.50 mg/individual/day (LSD Fisher p < 0.0001). The interaction between the plant species factor and the stage of development was significant. Adult individuals had a -superior AD with soybean than with the other three plants;, and in the nymphal instars, the AD was higher in oat than in corn and soybean but similar to wheat.

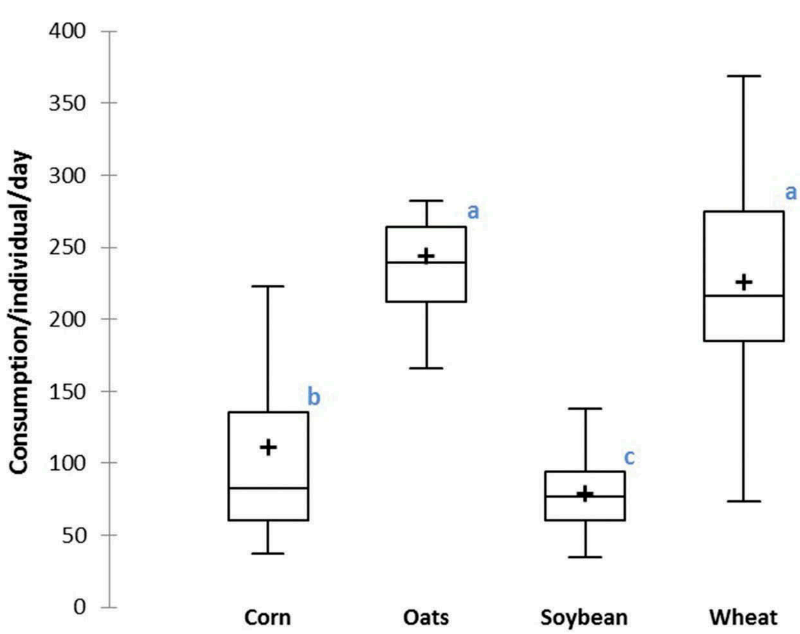

Figure 4. Relative consumption rate (mg/individual/day) of *Dichroplus maculipennis* according to plants species at laboratory conditions (30ºC, 14L:10D). Different letters indicate significant differences (LSD Fisher p < 0.05).

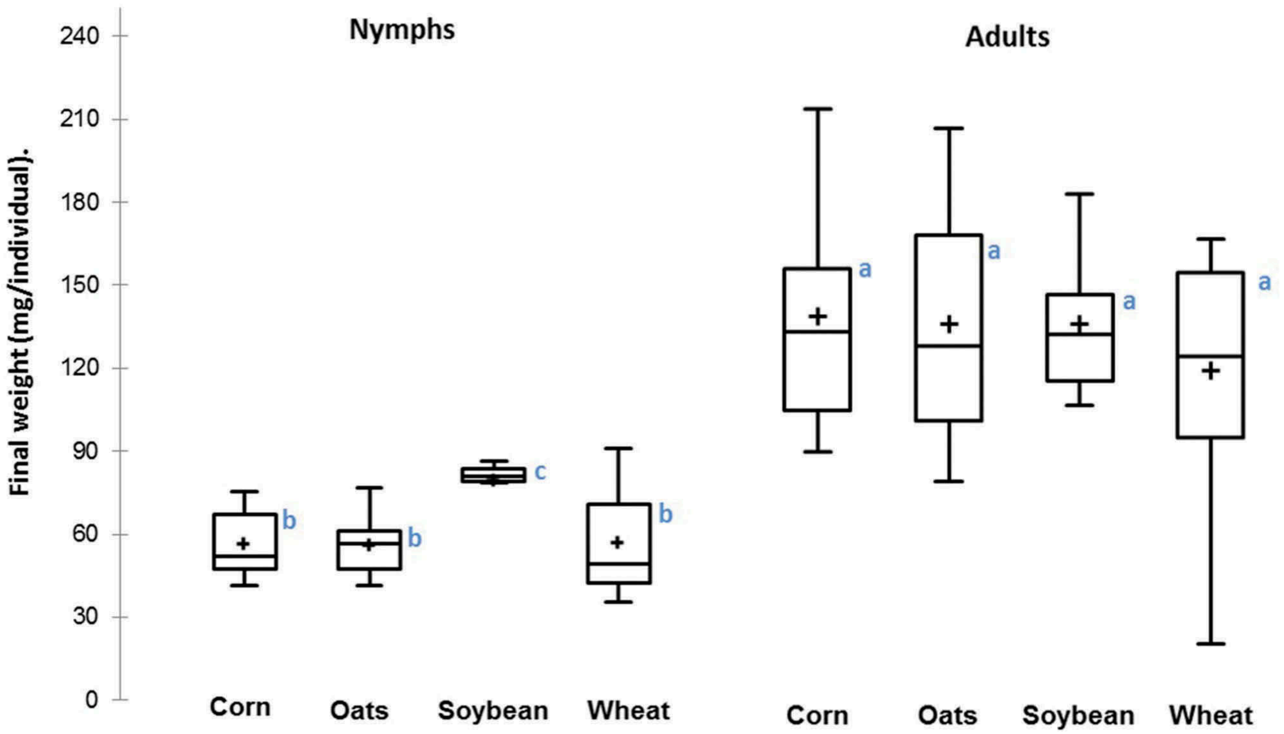

Figure 5. Mean final weight reached by nymphs and adults of *Dichroplus maculipennis*, according to plants species at laboratory condition (30ºC; 14L: 10D). Different letters indicate significant differences (LSD Fisher $p < 0.05$).

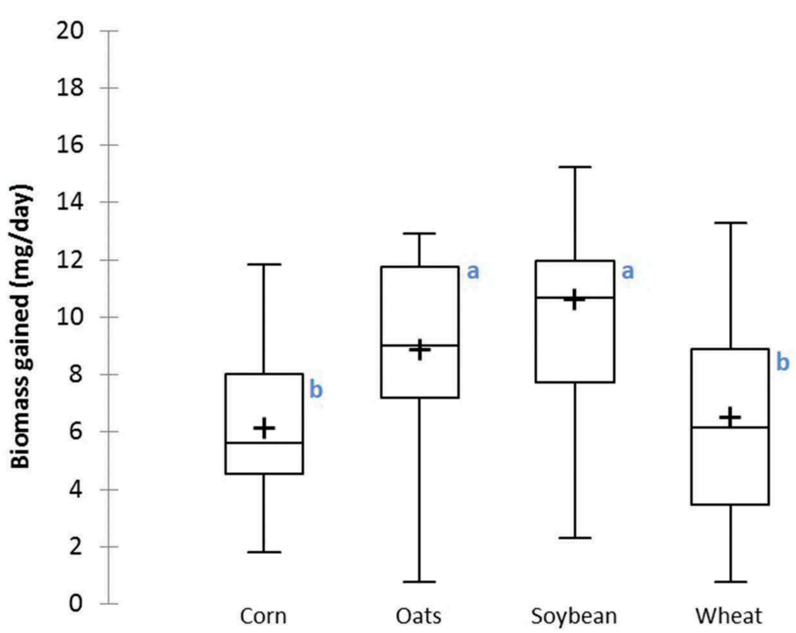

Figure 6. Mean biomass gained by individuals of *Dichroplus maculipennis* according to plant species, at laboratory condition (30ºC; 14L: 10D). Different letters indicate significant differences (LSD Fisher $p < 0.05$).

Discussion

Herbivores normally have to balance the intake of different nutrients for successful development; these include amino acids, sterols, phospholipids, carbohydrates, fatty acids, minerals, vitamins, trace elements and water. Plants contain all these nutrients, but the ratios and absolute amounts of these can be very variable. The variation is highest between different plant species, but also within species due to differences in genetic and environmental conditions (Behmer 2009). In general, it is considered that forbs are relatively higher in protein content than grasses, which would be one of the reasons why forbs are better quality food for most herbivores (Franske et al. 2010). The nutritional analysis made on the plants used in this study showed that the amount of nitrogen present in soybean (forb) was approximately twice that found in the other species (grasses). Nevertheless, Jonas and Joern (2008) mentioned that mixed-feeding herbivores have a higher performance when both forbs and grasses are consumed. The individuals of *D. maculipennis* –regardless of sex and developmental stage – consumed the four species of plants offered but in different amounts; the consumption rate values *per* individual indicated that the more consumed species were oat and wheat, then corn, and finally soybean. One possible reason for soybean avoidance could be the plant´s structural traits that form the first physical barrier to herbivores´ feeding (hardness of leaves, presence of trichomes) as pointed out by different authors (Bernays & Chapman 1970; Miura & Ohsaki 2004; War et al. 2012).

On the other hand, taking into account the nutritional composition of the plants, different studies discuss the fact that some animals regulate intake of multiple nutrients independently and instead of maximizing intake avoid ingesting surpluses and deficits relative to regulated points (Raubenheimer & Simpson 1997; Simpson & Raubenheimer 2001). This nutritional target can be effectively stabilized over a wide range of food protein and carbohydrate compositions. Due to the interplay of several behavioral mechanisms which include selection among unbalanced but complementary resources (Chambers et al. 1995; Behmer et al. 2001; Lee et al. 2002), compensatory feeding by adjusting total amount of food ingested (Raubenheimer & Simpson 1993), and post-ingestion regulation (Zanotto et al. 1993, 1997). Since soybean was the highest food quality species analyzed individuals might have made a lower consumption of it because with less quantity ingested they would satisfy their nutritional needs. In other words, soybean seems to be the more ‘nutritionally balanced food’ among the plants offered. The higher consumption registered in oat (the plant with the lowest nitrogen content in this study) with respect to soybean might indicate a compensatory feeding response. Different authors have indicated that a way of stabilizing nutrient intake, and thus growth and development performance, is through compensatory feeding (Bernays & Chapman 1973; Yang & Joern 1994). Raubenheimer (1992) showed for both low-nitrogen and low-carbohydrate diets a significant increase in consumption of *Locusta migratoria*, suggesting a compensatory feeding response to both nutrients. Berner et al. (2005) registered that the overall mean food consumption of the grasshopper *Omocestus viridulus* feeding on low nitrogen grass was 82% higher than on fertilized grass.

Female adults of *D. maculipennis* had a higher relative consumption rate than male adults, which could be related to reproductive aspects. According to Lockwood et al. (1996), females consume a greater amount of food than males because they have higher protein demands for egg production. Similar results were obtained when other species of grasshoppers were evaluated (de Wysiecki 1986; Sánchez and de Wysiecki 1990; Gangwere et al. 1997; Capello et al. 2011; Mariottini et al. 2011).

The highest relative growth values were observed in adult females, and this is probably related to the finding that this development state has the highest consumption *per* gram of animal. The covariate used in the analysis ‘initial weight’ was significant, indicating that the weight of individuals influences the growth rate.

The growth rate obtained from individuals that were fed soybean was similar regardless of the sex and developmental stage. From this, it can be assumed that individuals consuming a significantly lower amount of soybean relative to oat and wheat may obtain the same biomass gain, or in other words, a similar relative growth rate. The results show that individuals that were fed soybean and oat had a superior growth rate than those which were fed wheat and corn.

Different authors indicate that the water content of plants influences the growth rate, a low water content acts as a limiting factor for the growth rate reduction of plant-fed caterpillars (Mattson & Scriber 1987; Shobana et al. 2010). In this study, no significant differences were observed in water content of the four plants, suggesting that it would not be a factor that makes a difference in the relative growth rate.

The Efficiency of conversion of ingested food (ECI) and the efficiency of conversion of digested food (ECD) of individuals of *D. maculipennis* varied significantly among the dependent variables used. Values of ECI and ECD were higher in nymphs than in adults. Köler et al. (1987) recorded a similar situation when they studied the food utilization efficiencies of three grasshopper species in the laboratory (*Chortippus parallelus, Chortippus biguttulus, Gomphocerinus rufus*). It was also registered that ECI and ECD values were higher when nymphs and adults fed on soybean, the species with highest nitrogen content, concurring with Loiza et al. (2008) who indicated that ECI and ECD generally increase in diets with higher protein. Bailey and Mukerji (1976) recorded that ECD values were lower in the grasshoppers *Melanoplus bivittatus* and *Melanoplus femurrubrun* feeding on corn and, due to a lower nutritional quality, grasshoppers that fed on this plant provided a significantly lower egg production when compared with those feeding on other diets. Miura and Ohsaki (2006) found that ECD was higher in individuals of the *Parapodisma subastris* that fed on qualitatively better plant species and food plant mixtures. Le Gall and Behmer (2014) studied the effects of protein and carbohydrate in *Melanoplus differentialis* and determined that consumption was high on foods with low macronutrient concentration, but the digestive efficiency was low.

The approximate digestibility (AD) represents the percentage of food ingested that is effectively assimilated by the insect. Here it was recorded that the amount of material consumed did not influence the AD values obtained. On the other hand, the values of AD were different between the developmental stages, the nymphs had a higher AD than the adult individuals. Other studies obtained similar results, Bailey and Mukerji (1976) recorded a decrease in AD with the nymphal development of the melanoplinos *M. vittatus* and *M. fermurrubrum*. Manoj et al. (2017) recorded a decrease in AD for *Chorthippus almoramus* from the fifth instars to adult on different plant species, in addition, they obtained higher values in males than in females. The latter was different from the result obtained in this study, where a greater AD was registered in the females of *D. maculipennis* with respect to the males.

The change of AD with age (development) is probably due to the selection of different parts of the foliage by the grasshoppers as they develop or that the younger stages fed on soft and more succulent tender leaves, whereas the adults fed on leaves which are more fibrous (Manoj et al. 2017). This situation does not reflect what happened in our study, where the different experiences are carried out at the same moment and both adults and nymphs are offered the leaves of plant species in the same stage of growth.

However, these results can relate, at least in part, to increased feeding rate and increased gut size when individuals grow. Shorter retention times and larger food mass would make enzymatic degradation and nutrient absorption through the gut wall less efficient as suggested by Schoonhoven et al. (2005).

The AD registered in the present study for *D. maculipennis* followed the same trend that food efficiencies are higher for females (adults and nymphs) fed soybean. In a study about the nutritional ecology of the Australian locust pest *Chortoicetes terminifera,* it was registered that, as the locusts increased in age, growth and dry matter consumption increased per unit body weight but diet digestibility and the rate of digestion decreased, resulting in the amount assimilated remaining the same (Clissold 2003).

The results obtained in this study represent the first knowledge about food utilization efficiencies of *D. maculipennis.* The results found here are mainly for short-term responses. Future studies of *D. maculipennis* life cycle related to the plants from which it feeds under field conditions should be conducted and will be evaluated long-term responses that determine individuals' fitness, such as survival, development time, and fecundity. As regards this, we considered it necessary to combine the knowledge of laboratory and field of the nutritional ecology to gain a better understanding of insect herbivore performance by feeding.

Disclosure statement

No potential conflict of interest was reported by the authors.

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