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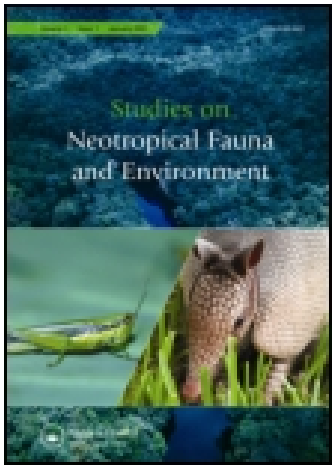


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# Phenotypic plasticity of the planthopper Delphacodes kuscheli (Hemiptera: Delphacidae) revealed by its selectivity, feeding rate and demographic traits on different food quality sites of wheat plants

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## ORIGINAL ARTICLE

# Phenotypic plasticity of the planthopper *Delphacodes kuscheli* (Hemiptera: Delphacidae) revealed by its selectivity, feeding rate and demographic traits on different food quality sites of wheat plants

María E. Brentassi[a]*, Gerardo Liljesthröm[b] & Ana M. Marino de Remes Lenicov[c]

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*Delphacodes kuscheli*, a phloem sap-sucking planthopper and the main vector of the Mal de Río Cuarto virus (MRCV) of maize in Argentina, was used to analyze phenotypic plasticity in behavior and demographic traits in response to different food quality, without masking the effects of density dependence and within-plant heterogeneity. We evaluated selectivity of nymphs and adults for different sites of wheat plants and, on sites suspected to have different food quality because of the presence/absence of meristems and therefore different nitrogen content, we evaluated pre-imaginal survival, nymphal developmental time, proportion of macropterous morphs, adult longevity and feeding rate. *Delphacodes kuscheli* showed a positive selection for plant zones suspected to have higher food quality and on them insects developed faster, exhibited higher nymphal survival and adult longevity and produced a lower proportion of macropterous morphs. Also on sites suspected to have lower food quality the number of honeydew droplets excreted per day increased and the mean diameter diminished, suggesting that the planthopper could probe more frequently to compensate for different food quality.

*Delphacodes kuscheli*, planthopper alimentador de savia y principal vector del Mal de Río Cuarto virus (MRCV) del maíz en Argentina, fue utilizado para analizar la plasticidad fenotípica en el comportamiento y características demográficas en respuesta a una diferente calidad alimenticia, sin los efectos enmascarados denso-dependientes y de la heterogeneidad de la planta. Evaluamos la selectividad de ninfas y adultos por diferentes sitios de las plantas de trigo y, sobre sitios de diferente calidad alimenticia, debido a la presencia-ausencia de meristemas y por lo tanto diferente contenido de nitrógeno, evaluamos la supervivencia pre-imaginal, tiempo de desarrollo ninfal, proporción de morfos macrópteros, longevidad del adulto y tasa de alimentación. *Delphacodes kuscheli* mostró selección positiva por sitios considerados de mayor calidad alimenticia y sobre ellos los insectos se desarrollaron más rápido, exhibieron una mayor supervivencia ninfal y longevidad del adulto y produjeron una menor proporción de morfos macrópteros. Además sobre sitios considerados de inferior calidad alimenticia el número de gotas de honeydew excretado por día incrementó y el diámetro disminuyó sugiriendo que el planthopper podría probar más frecuentemente para compensar la diferente calidad alimenticia.

**Keywords:** food quality; planthoppers; phenotypic plasticity; nitrogen; Mal de Río Cuarto virus; maize

## Introduction

Phenotypic plasticity is the capacity of a genotype, owing to environmental influences, to vary and exhibit different phenotypes (DeWitt & Langerhans 2004). The concept was first applied to morphological traits (Schlichting & Pigliucci 1998), but it is generally accepted that phenotypic plasticity can manifest as changes in biochemistry, physiology, behavior, and life history in response to the environment (Agarwala 2007). It is beneficial when it allows an individual to alter its phenotype to adaptively match a changing environment; however, phylogenetic constraints clearly prohibit certain plasticities. Phenotypic plasticity can be permanent or reversible, and the timing, specificity, and speed of plastic responses are critical to their adaptive value (Whitman & Agrawal 2009). Because phenotypic plasticity can increase fitness in multiple environments, it may also widen niche breadth, aid dispersal and widen geographic range (Schlichting 2004; Pigliucci et al. 2006). Species vary greatly as to when in their development they can respond to environmental change (Whitman & Agrawal 2009). In some species, developmental processes create specific windows when plasticity is possible; this occurs

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particularly in arthropods because of their discrete life stages and their external skeleton, which is not amenable to change after sclerotization (Frankino & Raff 2004). Many species have evolved precise temporal windows of responsiveness, and if they do not receive the appropriate environmental stimuli during that critical period, plasticity does not occur; examples are some butterfly polyphenisms (Nijhout 2003).

A typical environmental influence is food quality, which can affect nearly every aspect of an animal's phenotype and ecology (van Kleunen & Fischer 2005). There may be different reasons for food quality heterogeneity: restricted transport of nutrients to specific aerial subunits by vascular architecture (Orians & Jones 2001), secondary chemistry of leaves (Hartley & Jones 1997), phenology and tissue developmental stage (young and old leaves), effects of abiotic environmental factors (leaves in sun or shade) and the presence of growing meristems (Denno & McClure 1983). In herbaceous plants the presence of growing meristems (e.g. in the leaf-axil) is associated with high nitrogen content, which is a limiting factor for many herbivores (Mattson 1980).

Among herbivorous insects, sap-feeding Hemiptera such as planthoppers tend to ingest large quantities of phloem sap to obtain sufficient nitrogen from it and eliminate much of the excess of water and sugars as honeydew droplets (Cook & Denno 1994). In some polymorphic species of planthoppers, feeding and development of nymphs on nitrogen-rich plants or nitrogen-rich plant parts were associated with increased feeding rate and performance and an increased proportion of brachypterous adults (Denno & Roderick 1990; Cook & Denno 1994; Lu & Heong 2009). In contrast, when grown in low quality habitats, these planthoppers exhibited an increased proportion of macropterous adults with larger thoraces, fully developed wings and thus a higher dispersal capability than the brachypterous morphs (Denno & Roderick 1990; Zera & Denno 1997; Benard & McCauley 2008). In macropterous morphs, the energy used to construct wings and wing muscles and to fuel the flight process may not be available for reproductive investment and a trade-off arises between flight capability and reproduction (Denno et al. 1989; Zera & Denno 1997). This explains the lower fecundity and the longer preoviposition period exhibited by macropterous females of some planthopper species (Denno & Roderick 1990).

Delphacidae is the most important family of the Fulgoroidea in an agricultural context and includes planthopper species that primarily feed and develop on monocotyledoneous plants (Cook & Denno 1994). Among them, *Delphacodes kuscheli* Fennah (Hemiptera: Delphacidae) is a multivoltine species widely distributed in Argentina (latitude 32° S to 35° S) that feeds on different cultivated and wild plant species (Remes Lenicov & Virla 1999). Nymphs are active and able to walk along the stem and leaves of the host plant. They undergo five instars, the longest of which is the fifth whose duration represents approximately 30% of the entire nymphal stage (Virla & Remes Lenicov 1991). The adults show wing dimorphism with brachypterous and macropterous forms of similar longevity (Remes Lenicov et al. 1991). *Delphacodes kuscheli* is a phloem feeder with the typical salivary-sheath feeding behavior (Brentassi 2004; Brentassi & Remes Lenicov 2007), an energy-demanding activity due to the formation of lipoproteinaceous salivary deposits, which remain in the plant tissue after the withdrawal of the stylets (Miles 1972). The insects are the most important vectors of the Mal de Río Cuarto virus (MRCV), a fijivirus (Reoviridae) that seriously affects maize (*Zea mays* L.) production in northern and central provinces of Argentina (Remes Lenicov et al. 1985; Lenardón et al. 1987; Remes Lenicov & Paradell 2012). This disease has also been detected in Uruguay (Ornaghi et al. 1999). Virus transmission occurs in spring when macropterous adults disperse to feed on juvenile maize plants due to the senescence of winter grasses, which generally serve as reservoirs of MRCV and are preferential hosts for *D. kuscheli* (Tesón et al. 1986; Remes Lenicov et al. 1991; Ornaghi et al. 1993; Grilli & Gorla 2002).

Although *D. kuscheli* is a serious pest, very little is known about its phenotypic plasticity to environments differing markedly in their food quality, both in space and time, such as agroecosystems. The objective of this study was to analyze the phenotypic plasticity of *D. kuscheli* in terms of its behavioral selectivity, feeding rate and demographic traits of single individuals fed on plant sites suspected to have marked differences in nutritional value because of the presence or absence of meristems, without the possibly masking effects of density dependence and within-plant heterogeneity.

## Materials and methods

### *Plants and insects used in the experiments*

We used wheat plants (*Triticum aestivum* L., Tala Dekalb® variety) (Family Poaceae) grown from seeds provided by the Experimental Station of Santa Catalina (FCAyF, UNLP), Argentina. Plants were grown individually in a 100 ml plastic pot filled with fertile soil under uncontrolled conditions in a greenhouse and irrigated when necessary. Each wheat plant used in the experiments is formed, like other grasses,

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by different growth units called tillers and each one consists of a series of phytomers, which form the basic growth unit, made up of a node, an internode, an axillary bud and an expanded leaf (Briske 1991; Moragues & McMaster 2012). Each expanded leaf is divided at the ligule – a membranous translucent structure – into two parts: a lower portion rolled into a tube-like form called the leaf sheath, and the leaf blade or lamina. There is an intercalary meristem at the base of the leaf sheath, and another one, called a collar, near the ligule at the base of the leaf blade, which allows the leaf expansion (Langer 1979). Like a telescopic structure, younger leaf sheaths are partially covered by leaf sheaths of older leaves.

For the experiments we used single vegetative tillers with four expanded leaves and a fifth non-expanded one. At this stage the nodes were not visible (Figure 1). The founding insects (nymphs and adults of *D. kuscheli*) were collected in 2011 on oat fields in Río Cuarto (Córdoba, Argentina), the endemic area of MRCV. They were carried to the laboratory at the Entomology Division (FCNyM-UNLP) and reared on oat at 24 ± 2°C, 50–60% RH and a L16:D8 photoperiod. To avoid previous generation diet effects, the insects were transferred and maintained on wheat plants for two generations before experiments (McNeely & Singer 2001).

### *Selectivity on wheat plants*

Wheat plants were enclosed individually within a polyethylene terephthalate (PET) cylinder, 30 cm in height and 12 cm in diameter, with a top opening covered by a fine mesh (Brentassi 2004). In each cylinder only one insect was introduced in order to avoid possible density-dependent effects. We performed two sets of experiments: in one set we used third instar nymphs and in the other 2–3-day-old macropterous adult females of *D. kuscheli*. In each of the four expanded leaves we defined the following plant zones: (i) the leaf sheath, 3–4 cm long, excluding the upper 0.5 cm contiguous to the ligule; (ii) the ligular zone, which includes the intercalary meristem adjacent to the ligule, the upper 0.5 cm of the leaf sheath and the basal 0.5 cm of the leaf blade; (iii) the lower half of the leaf blade excluding the 0.5 cm basal length mentioned above; (iv) the upper half of the leaf blade; and (v) the fifth non-expanded leaf (Figure 1).

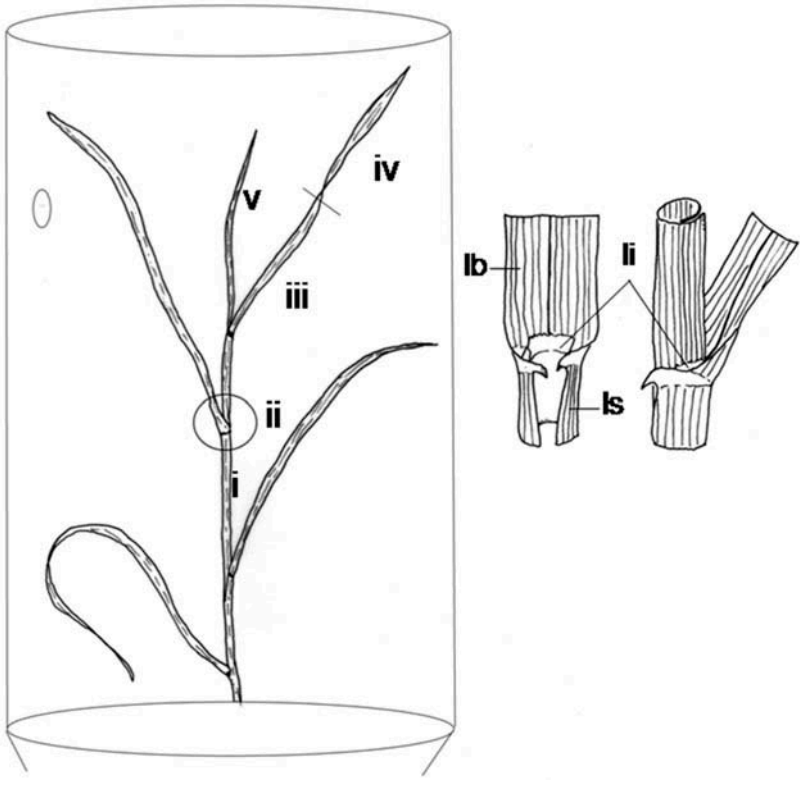


Figure 1. Zones defined on *Triticum aestivum* L. plants: i, leaf sheath (3–4 cm length) excluding the upper 0.5 cm below the ligule; ii, ligular zone (enlarged area) which includes the intercalary meristem (collar) adjacent to the ligule (li), the upper 0.5 cm length of the leaf sheath (ls) and the basal 0.5 cm of the leaf blade (lb); iii, lower half of the leaf blade (excluding the 0.5 cm length mentioned above); iv, upper half of the leaf blade; v, non-expanded leaf.

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The areas were expressed in $cm^2$ and were calculated as follows: the leaf sheath was considered as a cylinder and its length and its diameter were measured with a millimeter ruler. The area of the ligular zone was calculated as the cylindrical area of the leaf sheath (0.5 cm length) plus the basal area of the leaf blade (0.5 cm length). The areas of the lower and upper halves of each leaf blade (excluding the basal 0.5 cm length) as well as the area of the non expanded leaf were calculated by means of a leaf area meter LI-COR 3000 (Lincoln, NE, USA) and the adaxial and abaxial leaf areas were considered to have the same surface. These calculations were made on plants similar to those used in the experiments with insects, and the total surface corresponding to the four zones of each of the four expanded leaves and the fifth non-expanded one allowed us to calculate the relative surface of each one, S*i*, where $i = 1$ to 5, representing the five plant zones.

Two hours before the observations, one insect per plant was released by means of an aspirator through a small hole in the plastic cylinder (Figure 1). For both developmental stages we released 10 insects in as many plants (repetitions), and in each plant we made 10 observations at 1 h intervals, registering the zone where each insect was settled and the height in cm from the ground level of the pot. From the total number of observations per plant we calculated the relative number of cases an insect was registered on the *i*th zone, *Di*. Adult and nymphal selectivity for the *i*th zone was estimated using the forage ratio (FR) selectivity index, FR*i* = D*i*/S*i*. The index takes values in the interval $(0, \infty)$, values smaller than one indicate negative selectivity, values equal to one indicate indifference, and values greater than one indicate positive selectivity (Cock 1978). The 10 successive observations in a given plant allowed us to calculate a unique FR value for each zone, which was considered a trial.

### *Demographic traits on different food quality plant zones*

We selected two plant zones that provided extreme values of the selectivity index from the second leaf, where most individuals concentrated: the ligular zone (selected) and the upper half of the leaf blade (avoided). Further, the ligular zone was suspected to have higher nutritional value than the upper half of the leaf blade because of the presence of an intercalary meristem (the collar) and hence more elevated nitrogen content (Langer 1979; Mattson 1980; Rademacher & Nelson 2001). The two zones were isolated by means of a cylindrical cage 3 cm in height and 1.5 cm in diameter, with both extremes covered with cotton and a lateral opening covered with a fine mesh (Figure 2). Plants of the same size and same phenological stage were assigned randomly to one of the two groups: in one group the cage was set at the ligular zone and in the other group the cage was set at the distal part (approximately 2.5 cm) of the upper half of the leaf blade.

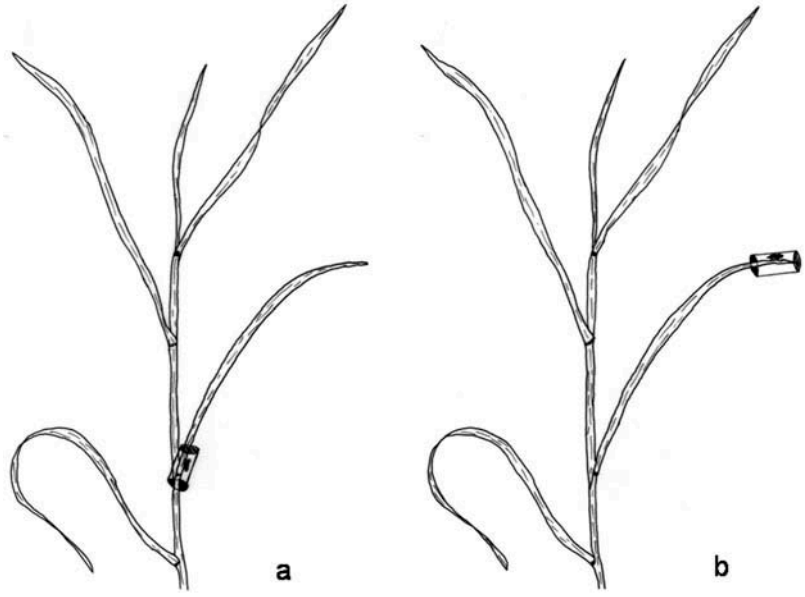


Figure 2. *Delphacodes kuscheli* females exposed individually to feed on two zones of wheat plants: a, ligular zone; and b, upper half of the second leaf blade.

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In order to prevent density-dependent effects, in each cage only one 0–1-day-old first instar nymph was introduced and feeding occurred only in the isolated site. To prevent the decay of plant quality due to caging and feeding, the cage and the insect from each plant were removed every two days and placed on a new plant on the corresponding zone. This procedure was repeated until the death of the insect. Each caged individual was considered a replicate and the initial number of first instar nymphs fed on the ligular zone or on the upper half of the leaf blade, were 15 and 18 respectively. Individual insects were checked daily for ecdysis in order to calculate the number of days in each developmental nymphal instar. Once in the adult stage, the insects were discriminated as macropterous or brachypterous and total body length from the tip of the head (vertex) up to the extreme of the abdomen as well as the wing length (from the tegula up to the apical extreme) were recorded under a binocular lens and expressed in mm.

The following demographic traits were estimated for nymphs fed on the ligular zone or on the upper half of the leaf blade: the duration of each nymphal stage and nymphal survivorship, the proportion of macropterous adults, adult longevity and adult length. Nymphal survivorship when fed on the $j$th zone ($j$ = 1, 2), NS$j$, was calculated as: NS$j$ = N$j_{(A)}$ /N$j_{(o)}$, where N$j_{(o)}$ represents the initial total number of 0–1-day-old first instar nymphs and N$j_{(A)}$ represents the corresponding total number of adults. The proportion of macropterous adults, when fed on the $j$th zone MA$j$, was calculated as: MA$j$/(MA$j$ + BA$j$), where MA$j$ and BA$j$ represent the total number of macropterous and brachypterous adults, respectively.

### *Feeding rate*

We further analyzed the daily feeding rate of adult insects when feeding on the ligular zone or on the distal part of the upper half of the leaf blade. On both selected zones, feeding rate was measured indirectly by assuming a positive relationship with honeydew excretion (Paguia et al. 1980; Padgham & Woodhead 1988). It was calculated by applying a modified method proposed originally by Khan & Saxena (1984). Macropterous females (0–2 d old) were individually caged and maintained feeding until they died: 15 females on the ligular zone and 10 females on the upper half of the leaf blade. As before, the insect in its cage was moved to the same position on a fresh plant every two days. To quantify daily honeydew excretion in the $j$th site, we recorded the diameter (expressed in mm) of each droplet glued to the cage walls by means of a graded ocular lens. Assuming a spherical shape, the volume of each droplet V$j$ was calculated as: $Vj = 4/3\pi r^3$, where r represents the radius of each droplet. Mean daily feeding rate F$j$ was calculated as: $Fj = \Sigma\,[Hdj \cdot Vmj]/\Delta t$, where Hd$j$ represents the total number of droplets glued on the cage walls, Vm$j$ represents the mean volume of the droplets and $\Delta t$ the interval, expressed in days, up to death of the insect. Additionally, we assumed that the mean daily feeding rate of a fifth instar nymph represents 0.59 of the mean daily feeding rate of a macropterous adult female as in the planthopper *Sogatella furcifera* (Horváth) (Zhu & Cheng 2002). So total food ingested during that instar when fed on the $j$th site was calculated by multiplying the mean daily feeding rate (0.59·F$j$) with the duration of the fifth nymphal instar. Because of its larger size and longer duration, total food ingested during the fifth nymphal instar would represent a great proportion of the food ingested during the nymphal stage.

We also analyzed possible relationships between the number of droplets excreted per insect (as the independent variable) and the mean diameter of droplets (as the dependent variable) by means of standard regression.

### *Statistical analyses*

All experiments were planned in a completely randomized design. The values of the selectivity index FR of *D. kuscheli* nymphs and adults for different sites of the host plant suspected to have distinct nutritional values were analyzed by means of ANOVA. When no transformation allowed homoscedasticity, the non parametric Kruskal–Wallis H test was used. Variations in total nymphal developmental time, adult longevity, adult size and volume of honeydew excretion were analyzed using one-way ANOVA. Developmental time of each nymphal instar was analyzed by one-way repeated measures ANOVA and sphericity was tested using the Mauchly test. Homogeneity of variance was analyzed using Levene's test: in the case of the duration of the nymphal stage, the inverse transformation of data allowed homoscedasticity; in the other cases no transformation was necessary. Differences between means were tested for significance with Tukey's honest significant difference (HSD). The proportion of nymphal survivorship and the proportion of adults that were macropterous (individual values were 0 or 1) were analyzed by means of GLM factorial model with binomial distribution and logit link function, with feeding place as the predictor variable. In a complementary analysis, the proportion of adults that were macropterous as well as between the proportion of nymphs that survive up to the adult stage were analyzed by the

normal deviate $Z$ test, $Z = [pL - pB]/\sqrt{([1(1 - pL)/nL] + [1(1 - pB)/nB])}$, where $pL$ and $pB$ represent the proportion when fed on the ligular zone and the upper half of the leaf blade, respectively, and $nL$ and $nB$ the corresponding number of cases.

We compared the mean daily feeding rate when fed on the ligular zone or on the distal part of the upper half of the leaf blade as well as total food ingested during the fifth instar using the $t$ test. In all statistical tests, $p < 0.05$ was considered significant (Scheiner & Gurevitch 2001).

## Results

### *Selectivity*

In both nymphs and adults of *D. kuscheli* the FR selectivity index was highest for the ligular zone and lowest for the upper half of the leaf blade (Tables 1, 2). In nymphs, the FR values differed significantly between treatments ($F_{(4,\ 45)} = 5.374$, $p = 0.0013$) and the HSD test indicated that selectivity for the ligular zone was higher than selectivity for the upper half of leaf blade ($p = 0.0019$) and the leaf sheath ($p = 0.0026$). In adults, the Kruskal–Wallis H test indicated significant differences between treatments ($H_{4,\ n=50} = 20.243$, $p = 0.0004$) and multiple comparisons indicated that the selectivity for the ligular zone was higher than for the upper half of the leaf blade ($p < 0.0005$) and the lower half of leaf blade ($p = 0.012$).

Regarding the vertical distribution of the insects on the wheat plant, we considered three strata: lower (0–8 cm); middle (8–16 cm) and upper (> 16 cm). The highest proportion of nymphs and adults (0.63 and 0.55 respectively) were recorded at the lower stratum (approximately at the level of the second and third leaf), and differences between both stages in three vertical strata were not significant ($X^2 = 4.892$, df = 3, $p > 0.05$) (Figure 3).

Table 1. Forage ratio (FR) selectivity index values of 10 *D. kuscheli* third instar nymphs for five zones of *Triticum aestivum* plants.

| | | | Leaf blade | | |
|---|---|---|---|---|---|
| Individuals | Leaf sheath | Ligular zone | Lower half | Upper half | Fifth non-expanded leaf |
| Nymph 1 | — | 4.18 | 0.53 | 1.05 | — |
| Nymph 2 | — | 2.74 | 0.92 | 1.38 | — |
| Nymph 3 | — | 0.73 | 3.31 | — | — |
| Nymph 4 | — | 2.19 | 2.57 | — | — |
| Nymph 5 | — | 2.19 | 1.47 | — | 3.22 |
| Nymph 6 | 3.1 | 1.46 | 0.37 | — | — |
| Nymph 7 | — | 1.99 | 2.34 | — | 0.98 |
| Nymph 8 | — | 2.92 | 2.21 | — | — |
| Nymph 9 | — | 2.92 | — | — | 6.44 |
| Nymph 10 | — | 7.31 | — | — | — |
| Mean ± SD | 0.31 ± 0.98 | 2.86 ± 1.82 | 1.37 ± 1.18 | 0.24 ± 0.52 | 1.06 ± 2.15 |

Table 2. Forage ratio (FR) selectivity index values of 10 *D. kuscheli* adults (2–3 d old) for five plant zones of *Triticum aestivum* plants.

| | | | Leaf blade | | |
|---|---|---|---|---|---|
| Individuals | Leaf sheath | Ligular zone | Lower half | Upper half | Fifth non-expanded leaf |
| Adult 1 | 2.53 | 1.23 | 1.01 | — | — |
| Adult 2 | 0.74 | 4.30 | 1.18 | — | — |
| Adult 3 | — | 5.38 | — | 0.44 | 2.64 |
| Adult 4 | 0.63 | 3.69 | — | 0.51 | 3.02 |
| Adult 5 | 1.11 | 4.30 | — | — | 2.64 |
| Adult 6 | 2.53 | 2.46 | 0.51 | — | — |
| Adult 7 | 1.48 | — | 0.59 | 1.18 | 1.76 |
| Adult 8 | 0.89 | 6.88 | — | — | — |
| Adult 9 | 1.77 | 3.44 | 0.71 | — | — |
| Adult 10 | 1.11 | 2.15 | 0.89 | — | 2.64 |
| Mean ± SD | 1.28 ± 0.98 | 3.38 ± 2.01 | 0.49 ± 0.46 | 0.21 ± 0.39 | 1.27 ± 1.38 |

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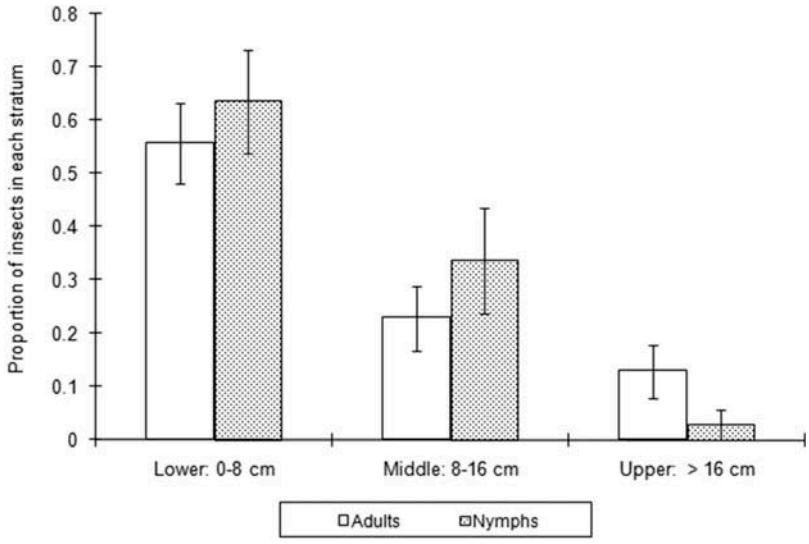


Figure 3. Vertical distribution of nymphs and adults of *D. kuscheli* in three strata of wheat plants. The bars on the columns indicate the standard error (SE).

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### *Demographic traits*

Total duration of the nymphal stage was significantly longer when insects fed on the distal part of the upper half of the leaf blade (20.85 d) than on the ligular zone (15.28 d) ($F_{(1,19)}$ = 13.78, $p$ < 0.001) and differences in duration between treatments were significant in the second and the fifth instars: ($F_{(1,19)}$ = 10.7012, $p$ < 0.004) and ($F_{(1,19)}$ = 12.7099, $p$ < 0.002) respectively (Table 3). The proportion of nymphal survivorship when fed on the ligular zone (0.93) was higher than when fed on the distal part of the upper half of the leaf blade (0.38) ($Z$ = 5.214, $p$ < 0.005). Only in the second instar the difference in the proportion of nymphal survivorship was significant ($Z$ = 4.54, $p$ < 0.001) (Table 4).

A higher proportion of macropterous adults emerged when nymphs were fed on the upper half of the leaf blade (1.0) than on the ligular zone (0.5) ($Z$ = 2.646, $p$ < 0.005) (Table 5).

Table 4. Survivorship of each nymphal instar and whole nymphal stage when fed on the ligular zone or the upper half of the second leaf blade of *Triticum aestivum* plants.

| Nymphal instar and whole nymphal stage | Ligular zone | Upper half of leaf blade | $Z$ | $p$ |
|---|---|---|---|---|
| 1st instar | 1 | 0.89 | 1.5 | 0.2> $p$ >0.1 |
| 2nd instar | 1 | 0.44 | 4.54 | < 0.001 |
| 3rd instar | 1 | 1 | — | > 0.7 |
| 4th instar | 0.93 | 1 | –1.4 | 0.2> $p$ >0.1 |
| 5th instar | 0.93 | 0.71 | 1.16 | 0.3> $p$ >0.2 |
| Whole nymphal stage | 0.93 | 0.38 | 5.21 | < 0.005 |

In order to analyze possible effects of both sex and morph type on adult longevity, we compared those adults fed only on the ligular zone: the males lived longer than females (28.0 d, SE = 3.79; and 18.33 d, SE = 1.78, respectively) ($F_{(1,\ 9)}$ = 6.146, $p$ = 0.035), while longevity did not differ significantly between

Table 3. Total duration in days (mean ± SE) of each nymphal instar and whole nymphal stage when fed on the ligular zone or the upper half of the second leaf blade of *Triticum aestivum* plants.

| Nymphal instar and whole nymphal stage | Ligular zone | Upper half leaf blade | $F$ | $p$ |
|---|---|---|---|---|
| 1st instar | 3.14 (0.22) | 3.42 (0.32) | $F_{(1,19)}$ = 0.5390 | 0.4718 |
| 2nd instar | 1.71 (0.15) | 2.71 (0.29) | $F_{(1,19)}$ = 10.7012 | < 0.004 |
| 3rd instar | 2.29 (0.26) | 2.57 (0.37) | $F_{(1,19)}$ = 0.3897 | 0.5399 |
| 4th instar | 3.21 (0.17) | 3.57 (0.25) | $F_{(1,19)}$ = 1.4012 | 0.2511 |
| 5th instar | 4.93 (0.20) | 8.57 (1.43) | $F_{(1,19)}$ = 12.7099 | < 0.002 |
| Whole nymphal stage | 15.28 (2.02) | 20.85 (0.40) | $F_{(1,19)}$ = 13.78 | < 0.001 |

Table 5. Number of adults, emerged on the ligular zone and or the upper half of the leaf blade, discriminating sex an morph type.

| | Ligular zone | | Upper half leaf blade | |
|---|---|---|---|---|
| | Macropterous | Brachypterous | Macropterous | Brachypterous |
| Females | 5 | 4 | 2 | — |
| Males | 2 | 3 | 5 | — |

morphs: brachypterous (19.5 d, SE = 2.29) and macropterous (22.86 d, SE = 4.72) ($F_{(1,\ 9)}$ = 1.247, $p$ = 0.293) and the interaction between sex and morph was also not significant ($F_{(1,\ 9)}$ = 0.158, $p$ = 0.700). The duration of the nymphal stage of individuals fed on the ligular zone was not affected by the morph type once in the adult stage: in macropterous individuals (both sexes) it was 15.571 d, SE = 0.52, while in brachypterous individuals (both sexes) it was 15.0 d, SE = 0.61 ($F_{(1,\ 12)}$ = 0.495, $p$ = 0.496).

When analyzing the effect of plant zone on male adult longevity we found that those individuals fed on the distal part of the upper half of leaf blade did not live as long (10.2 d, SE = 1.39) as those fed on the ligular zone (21.2 d, SE = 2.12) ($F_{(1,\ 5)}$ = 15.389, $p$ = 0.011).

For the macropterous adults, wing length was correlated with body length and females were longer than males (Figure 4), but the plant zone where the insects of a given sex were fed did not significantly affect their body length. When fed on the distal part of the upper half of leaf blade or on the ligular zone, the body length of macropterous males was 2.21 mm (SE = 0.087) and 2.46 mm (SE = 0.15), respectively ($F_{(1,\ 5)}$ = 2.2806, $p$ = 0.191), while the length in macropterous females was 2.63 mm (SE = 0.01) and 2.77 mm (SE = 0.06), respectively ($F_{(1,\ 5)}$ = 2.163, $p$ = 0.201).

### *Honeydew excretion rate*

Daily honeydew excretion per adult female when fed on the distal part of the upper half of the leaf blade (0.397 $mm^3$/day, SE = 0.05) did not differ significantly from those fed on the ligular zone (0.466 $mm^3$/day, SE = 0.04): ($F_{(1,\ 20)}$ = 1.2802, $p$ = 0.271), and the mean diameter per droplet diminished as the total number of droplets excreted per day increased: Y = 0.7179 – 0.0016 X ($t_{20\ df}$ = –3.791, $p$ < 0.0012). Considering the fifth instar nymphs,

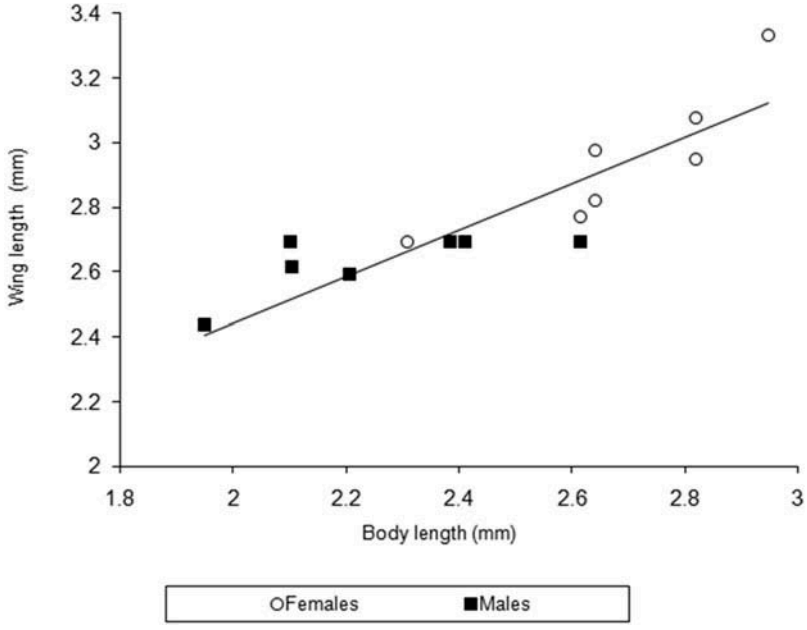


Figure 4. Relationship between wing length as the dependent variable and body length as the independent variable (in mm) of macropterous adults: $y$ = 0.7184 $x$ + 1.0063, $r^2$ = 0.809, $t$ (12 df) = 7.121 ($p$ < 0.00001).

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honeydew excretion rate when fed on the upper half of the leaf blade (2.01 $mm^3$, SE = 0.25) was 47.9% higher than that of insects fed on the ligular zone (1.42 $mm^3$, SE = 0.09) ($t_{19\ df} = -2.756$, $p = 0.013$, two tailed test).

## Discussion

### *Selectivity*

Values of the selectivity index allowed us to identify the ligular zone, which includes an intercalary meristem, the basal half of leaf blades and the non-expanded fifth leaf as the selected zones. However, because we were unable to discriminate feeding from other activities of the insects such as mate-searching, habitat exploring or resting, selectivity is considered in a broad sense. It has been suggested that the leaf axils at the leaf-blade junction have a high nutritional value because of the presence of the meristem and hence more elevated nitrogen content (Langer 1979; Mattson 1980; Rademacher & Nelson 2001). Similar studies on the Russian wheat aphid *Diuraphis noxia* (Mordvilko) (Hemiptera: Sternorrhyncha: Aphididae) showed that non-expanded (= growing) wheat leaves and the junction between the blade and the sheath of mature leaves (just above the ligule) were two preferred microsites for feeding (Clark & Messina 1998). Furthermore, the selection of other nitrogen-rich feeding sites on host plants, such as young leaves, buds and inflorescences, has also been reported for several delphacid species as an adaptation to minimize the nitrogen shortage (Cook & Denno 1994).

The nymphs and adults of *D. kuscheli* settled preferentially in the lower stratum of wheat plants (approximately at the level of the second and third leaf). A vertical distribution was also observed for the endophytic eggs deposited by females of *D. kuscheli* in barley (*Hordeum vulgare* L.) plants, the vast majority of which were distributed in the ligular zone and the lower half of the fourth leaf blade (Brentassi & Remes Lenicov 1999). Similar distributions of individuals on the lower plant stratum was detected in different species of delphacids and cicadellids (Hemiptera: Auchenorrhyncha) and the distribution was related to microclimatic conditions and physiological or structural characteristics of the host plant which could allow insects to hide from their natural enemies (Denno & Roderick 1990; Cook & Denno 1994).

### *Demographic traits*

Feeding of *D. kuscheli* on the ligular zone resulted in a shorter duration of nymphal development, decreased nymphal mortality, higher adult longevity and lower proportion of macropterous morphs, suggesting that this part of the plants has a higher nutritional value for *D. kuscheli.* Similarly Wang et al. (2006) showed that the delphacid *Peregrinus maidis* (Ashmead) growing on plants with higher nitrogen concentrations had a significantly shorter development time, higher immature survival rate and adult longevity, and that the intrinsic rate of population increase was positively correlated with the nitrogen levels in the treated plants. Similar results reported by Lu et al. (2004) showed that the delphacid *Nilaparvata lugens* (Stål) not only exhibited a preference for fertilized rice plants but also increased its reproductive potential when fed on those plants. In addition Mattsson (1980) and Cook & Denno (1994) showed that, with similar feeding rates, herbivores and specifically delphacids that feed on nitrogen-poor environments exhibit slower growth and longer generation times. In addition, adult body size of *D. kuscheli* fed on the ligular zone tended to be larger (although not significantly) than individuals fed on the upper half of the leaf blade. Denno & McCloud (1985) argued that increased body size of the delphacid *Prokelisia marginata* (Van Duzee) was directly related to the better resource quality, and a positive relationship between body size and fecundity was reported. In fact, the delphacid *Dicranotropis hamata* (Boheman) showed higher fecundity when fed on plants with high nitrogen levels (Cook & Denno 1994).

Regarding wing dimorphism, we found that the proportion of macropterous morphs was higher on the upper half of leaf blade, suggesting that the resource quality could be influencing the proportion of wing morphs in *D. kuscheli.* Furthermore, Remes Lenicov et al. (1991) showed that during spring, when oat (*Avena sativa* L.) was in the reproductive stage, the percentage of brachypterous females was above 60%. This could be related to a higher resource quality of the host plant during spring; in grasses, the levels of free amino acids increase in spring as metabolites are transported to the growth zones and inflorescences for the grain growth (Briske 1991). Wing form in planthoppers is determined by a complicated interaction between environmental cues such as crowding and host plant quality and genetic factors (Denno & Roderick 1990). Denno et al. (1985) argued that in *Prokelisia* species as in most delphacids, production of macropterous morphs is influenced by inadequate nutrition due to nitrogen deficiency, age, senescence or wilting of the host plant.

### *Feeding rate*

The higher volume of food ingested during the fifth instar when feeding on the upper half of the leaf blade

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suggests that the insects could compensate for the presumably lower food quality by ingesting much more. Lu et al. (2007) reported that many insects modify the feeding rate in response to variation in food quality, especially on plants with low nitrogen content from which herbivores might take high amounts of food to meet their needs. The observed increase in the total number of droplets excreted and the decrease in diameter per droplet are likely due to increased probing of the plant tissues by the planthoppers in order to find good feeding sites. Due to the energy demand of feeding activity exhibited by *D. kuscheli* (Brentassi 2004), these results suggest that when a good feeding micro-site was detected, this planthopper could remain there for a long time, performing a sustained ingestion and probing less frequently than on lower quality feeding sites. Sogawa (1982) and Cook et al. (1987) found that *N. lugens* probed more frequently, ingested much less phloem sap and excreted much less honeydew when feeding on nitrogen deficient rice plants. Consistently Lu et al. (2005) and Lu & Heong (2009) reported that planthoppers probed less when feeding on high nitrogen plants.

### *Phenotypic plasticity*

Our findings show how phenotypic plasticity allows *D. kuscheli* to react to differences in food quality of its host plants. Behavioral plasticity is expressed in the selection by nymphs and adults of feeding sites assumed to have higher nitrogen content, and in adapting the frequency of probing of plant tissues to the nutritional quality of the food sites. Morphological plasticity is expressed in the switching towards macropterous or brachypterous adults according to the low or high food quality, respectively, experienced by the nymphs. This response would be highly adaptive as it allows morphs reared on poor quality hosts a wider foraging array in which to find and explore plants of high food quality. Our study suggests that *D. kuscheli* is sensitive to the food quality of their host plants. Therefore, future studies should seek to further clarify the effects of food quality, specifically nitrogen content, on life history traits of *D. kuscheli.*

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