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Do aphids maintain differential densities on plant parts? A case study with *Aphis craccivora* Koch (Hemiptera, Aphididae)

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ABSTRACT: Differential aggregation of aphids on host plant parts may indicate site-specific optimal densities for efficient utilization of plant parts, besides the usual inference of preferential colonization. Differential densities of aphids within the plant were studied using the legume aphid *Aphis craccivora* Koch in cowpea *Vigna unguiculata* (L.) Walp. ssp. *unguiculata*. In field-collected infested sample stems and pods (n=60), colonies were demarcated, aphid colony size, length and circumference measured, and colony area and density calculated. The results indicated that colony dimensions and colony size were significantly higher in pod than in stem whereas colony density did not differ significantly between the two plant parts. Colony density was significantly higher in leaflets of top most leaf than in leaflets of top 2nd or 3rd leaf. Overall, the four plant parts could be graded in the descending order as stem>pod>leaflets of top most leaf> leaflets of top 2nd or 3rd leaf for colony density. Significant positive curvilinear and linear relationship between colony size and colony density in both stem and pod indicated that *A. craccivora* showed a propensity to spread out colonies at low populations but tended to compact them with a rise in population levels. Identical colony density in stem and pod suggested that the aphid may not require differential densities to overcome host defenses or utilize food from these two plant parts. In top most leaf and top 2nd or 3rd leaf, finite leaflet size apparently limits proliferation of the aphid. Higher density on top immature leaves could be more an outcome of nutritional suitability than the need to overcome host defenses. Variable colony densities on the four parts of *V. unguiculata* indicated differential optimal densities.

KEY WORDS: *A*ggregation, cowpea, colony dimensions, optimal density

INTRODUCTION

The concept of optimal density range of organisms on exhaustible units of food resource (Peters and Barbosa, 1977) revolves around the premise that organisms maintain their densities between a minimum and maximum to offset the disadvantages of undercrowding and overcrowding, respectively (Prokopy, 1981). Although proposed for laboratory insect cultures (Peters and Barbosa, 1977), the concept has direct relevance to field populations of several groups of insects (Prokopy, 1981). Limited capability for successful dispersal among resource patches and other causes were suggested to subject

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a species to less selection pressure for early establishment of an optimal density range ultimately favoring a high degree of population clumping (Prokopy, 1981).

As *r*-strategists, the Sternorrhyncha, *e.g.* Aphidoidea, form aggregations on annual plants in short-lived crop systems and show increased fitness within optimal density ranges on host plants (Way and Banks, 1967; Dixon and Wratten, 1971). Aggregation of aphids confers benefits of greater ability to divert host nutrients from other leaves (Way and Cammell, 1970), besides enhanced protection from predators by aphid-tending ants (Nault *et al.,* 1976). Changes in the phloem amino acid composition of host plants induced by two species of aphids appeared to affect systemically at least the whole leaf they were feeding on with likely nutritional advantages for the aphids (Sandström *et al.,* 2000). Aphids are known to display preferences for different organs of the same plant. For example, *Aphis gossypii* G. preferred older leaves of tender plants of aubergine *Solanum melongena* L. (Banerjee and Raychaudhuri, 1985) and was most abundant on the basal part of cantaloupe vines *Cucumis melo* L. (Edelson, 1986). Besides preferential colonization governed by nutritional differences, differential colony size of aphids may indicate maintenance of site-specific optimal density ranges for utilization of plant parts and enhancement of survival and reproduction.

The legume aphid *Aphis craccivora* Koch (Hemiptera, Aphididae) maintains large aggregations (Srikanth and Lakkundi, 1988a; Srikanth, 2001) on individual plant parts of preferred annual plants like cowpea *Vigna unguiculata* (L.) Walp. ssp. *unguiculata* (Family: Fabaceae) (Srikanth and Lakkundi, 1988b), with the overall populations growing rapidly from vegetative stage to reproductive stage of the crop (Srikanth and Lakkundi, 1990). It is likely that optimal densities also change along with growth in aphid populations through different phenological stages of the host. Within-plant characterization of aphid colonies is likely to reveal the occurrence of differential densities which, in turn, would allow further studies to infer on feeding site preferences and optimal densities. Therefore, in the present study, the within-plant colonization pattern of *A. craccivora* in *V. unguiculata* was explored to hypothesize on the occurrence or maintenance of optimal densities of the aphid on different plant organs.

MATERIALS AND METHODS

Inter-organ variability in the colonies of *A. craccivora* was examined in the locally popular and aphid-susceptible cultivar C 152 of *V. unguiculata* raised in the field. While stem, pod, leaflets of top most leaf and leaflets of top 2nd or 3rd leaf hosting dense colonies were considered, middle and lower leaves were ignored as they harbored sparse aphid colonies. Colonies were treated as dense when the aphids were in close physical contact with one another, whose visual counting would surely be erroneous. On the other hand, sparse colonies were those whose members maintained some distance from their neighbors and could be easily counted visually. Samples of the four plant parts (n=60) were collected from pod formation to pod-filling stages as these phenological stages ensured abundant aphid populations and colonies on all parts of the plant.

Infested sample stems and pods of varying size and aphid intensity were detached carefully from the plant using a sharp razor blade, placed in plastic containers of suitable size and brought to the laboratory. In stems, since aphid aggregations extended across leaf nodes with gaps, two adjacent aggregations that were separated distinctly were regarded as independent colonies. Aggregations that covered young pods completely were taken as a single colony but those that covered mature pods with distinct gaps were considered independent colonies. After marking both ends of the colonized portion on stem or pod as colony boundaries, aphids from the colonized portion were dislodged on a sheet of white paper by tapping and brushing the aphids off the stem or pod using a fine camel hair brush, and their number was counted (hereafter colony size). The length (hereafter colony length) and circumference (hereafter colony circumference) of marked, i.e. colonized portion of stem or pod were measured and the surface area (hereafter colony area) of colonized portion was calculated; together, these three parameters constituted colony

dimensions. From colony size and colony area, aphid density per unit area (number cm^{-2}) (hereafter colony density) was estimated.

For characterization of colonies on leaves, aphid number (colony size) on leaflets of top most leaf and leaflets of top 2nd or 3rd leaf was counted (n = 60 leaflets) by dislodging the aphids on a sheet of white paper as described above. Since the leaflets of top most leaf could be covered easily by a 1 cm^2 window cut on paper, their area was assumed to be 1 cm^2. Consequently, colony density cm^{-2} on these leaflets was same as the colony size. Similarly, area of leaflets of the top 2nd or 3rd leaf was assumed to be 4 cm^2 after verifying that these leaflets could be covered by a window of 2 cm x 2 cm. Consequently, colony density per unit area (number cm^{-2}) was estimated as one-fourth of the colony size.

In preliminary examination of data, normal probability plots of the five colony parameters, namely colony length, circumference, area, size and density from 60 sample units for stem and pod indicated deviation from normality; the confirmatory Shapiro-Wilk W test established the same. Similar analysis of data of colony density on leaflets of top most leaf and leaflets of top 2nd or 3rd leaf also showed deviation from normality. In view of the non-normality of data, the non-parametric Mann-Whitney U test was used to compare the five colony parameters between stem and pod, and colony density between leaflets of top most leaf and leaflets of top 2nd or 3rd leaf. The colony parameter data from the four plant organs were also examined for skewness. Colony density on stem, pod, leaflets of top most leaf and leaflets of top 2nd or 3rd leaf was compared by non-parametric Kruskal-Wallis analysis of variance (ANOVA) and multiple comparison tests. The inter-relationships among colony length, colony circumference, colony area, colony size and colony density for stem and pod were examined by correlation and regression analysis. Normality and non-parametric tests were performed in StatSoft Inc. (2004) and correlation and regression analyses were carried out in TableCurve 2D (2002).

RESULTS AND DISCUSSION

Colony parameters of *A. craccivora*, with the exception of colony length, deviated significantly from normality in both stem and pod, as confirmed by Shapiro-Wilk W test (Table 1). The distribution of colony length and colony circumference was not skewed whereas colony area, colony size and colony density displayed significant positive skewness in stem and pod (Fig. 1, 2). Mean colony length, colony circumference, colony area and colony size were significantly higher in pod than in stem by Mann-Whitney U test (Table 2). Colony density on stem and pod, however, did not differ significantly despite the slightly higher mean and range in the former.

Colony size was, in general, significantly and positively correlated with colony dimensions in stem and pod with minor variations and a few exceptions

Table 1. Normality and skewness of colony characteristics of *Aphis craccivora* in *Vigna unguiculata* stem and pod

Parameter	Shapiro-Wilk W@		Skewness z#	
	Stem	Pod	Stem	Pod
Colony length (cm)	0.962^{ns}	0.978^{ns}	1.67^{ns}	1.11^{ns}
Colony circumference (cm)	0.954^{*}	0.940^{**}	0.26^{ns}	1.92^{ns}
Colony area (cm^2)	0.948^{*}	0.943^{**}	1.97	3.40
Colony size (no.)	0.875^{****}	0.884^{****}	4.68	4.34
Colony density (no./cm^2)	0.909^{***}	0.934^{**}	2.37	2.28

@ Shapiro-Wilk W: significance at $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.0001$; ^{ns} not significant $P > 0.05$;
# Skewness/SE of skewness; ^{ns} not significant ($z < \pm 1.96$), the rest are significant (Cramer and Howitt, 2004)

(Table 3). While colony length lacked significance in stem, colony circumference was not significant in pod. In contrast, colony density was negatively correlated with colony dimensions in both stem and pod with the exceptions of colony circumference in stem and colony length in pod. Colony density was significantly and positively correlated with colony size in stem and pod considered separately; the relationship was slightly stronger for stem than for pod (Table 3). The overall colony density vs. colony size relationship for the data pooled for stem and pod was also positive and significant ($r = 0.535$; $n = 120$; $P < 0.0001$). Colony density vs. log colony size linear relationship (Fig. 3) was stronger than

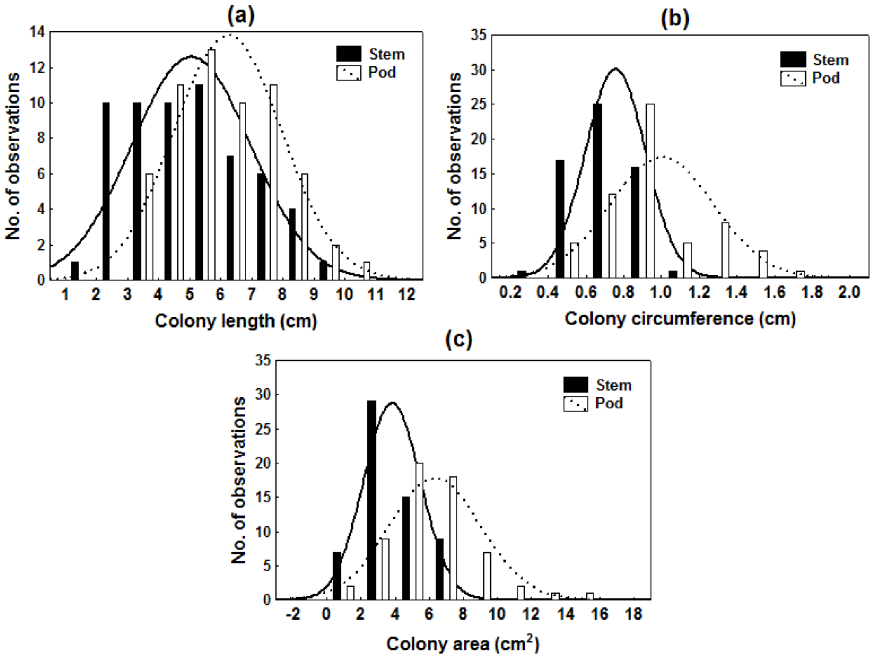

Fig. 1 Frequency distribution of *Aphis craccivora* colony dimensions in *Vigna unguiculata* stem and pod: (a) colony length (b) colony circumference (c) colony area

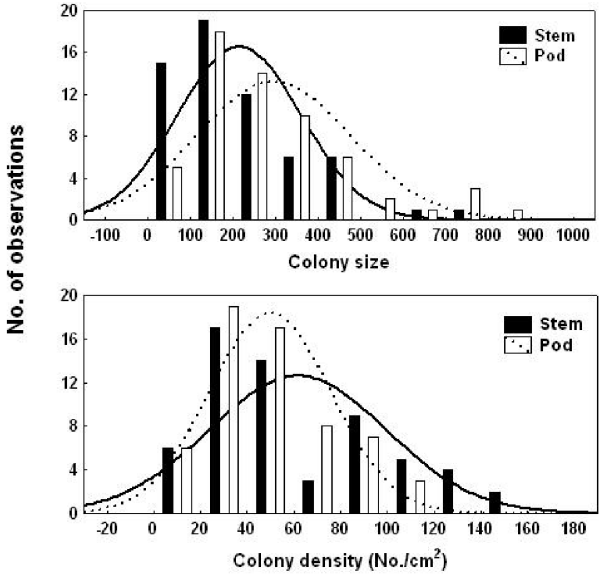

Fig. 2 Frequency distribution of *Aphis craccivora* colony size (top) and colony density (bottom) in *Vigna unguiculata* stem and pod

Table 2. Comparative colony characteristics of *Aphis craccivora* in *Vigna unguiculata* stem and pod

Parameter	Stem	Pod	Z value[@]
Colony length (cm)	5.03 ± 1.90[#] (2.00 - 9.80)[!]	6.21 ± 1.74 (3.20 - 10.60)	3.422***
Colony circumference (cm)	0.75 ± 0.16 (0.40 - 1.10)	1.00 ± 0.28 (0.50 - 1.70)	5.243****
Colony area (cm^2)	3.80 ± 1.66 (1.32 - 7.84)	6.29 ± 2.69 (1.60 - 15.90)	5.571****
Colon size (no.)	212.62 ± 144.67 (51.00 - 744.00)	293.08 ± 181.25 (71.00 - 878.00)	2.858**
Colony density (no./cm^2)	61.10 ± 37.93 (11.11 - 147.10)	49.45 ± 26.07 (14.12 - 111.87)	1.302ns

[#] Mean ± SD; n=60; [!]figures in parentheses are ranges[@] Mann-Whitney U test - Significance at ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ns $P > 0.05$

colony density vs. colony size relationship (Fig. 4) for both stem and pod. Colony density on leaflets of both top most and top 2nd or 3rd leaves deviated significantly from normality (Table 4) but did not skew significantly in both (Fig. 5). Colony density was significantly higher on leaflets of top most leaf than on leaflets of top 2nd or 3rd leaf. ANOVA comparison of colony density on all the four plant parts graded them in the descending order as stem, pod, leaflets of top most leaf and leaflets of top 2nd or 3rd leaf with some overlapping differences (Table 5). While colony density on stem was significantly higher than those on leaflets of both leaves, colony density on pod was significantly higher than that on leaflets of top 2nd or 3rd leaf alone.

Examination of colony characters of *A. craccivora* in *V. unguiculata* in the present study revealed interesting trends. The lack of skewness for colony length and colony circumference suggested that the aphid colonized and exploited stems and pods of diverse size or age and maturity randomly, under the pressure of growing populations at pod formation stage. On the contrary, non-normality and significant positive skewness of colony area, colony size and colony density indicated the tendency of the aphid

Table 3. Correlations among colony characteristics of *Aphis craccivora* in *Vigna unguiculata* stem and pod

Parameter	Size	Density
Stem		
Colony length	0.141ns	-0.468***
Colony circumference	0.530***	0.175ns
Colony area	0.377**	-0.312*
Colony size	-	0.690***
Pod		
Colony length	0.594***	-0.094ns
Colony circumference	0.242ns	-0.418**
Colony area	0.585***	-0.263*
Colony size	-	0.566***

Significance at * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns Not significant $P > 0.05$

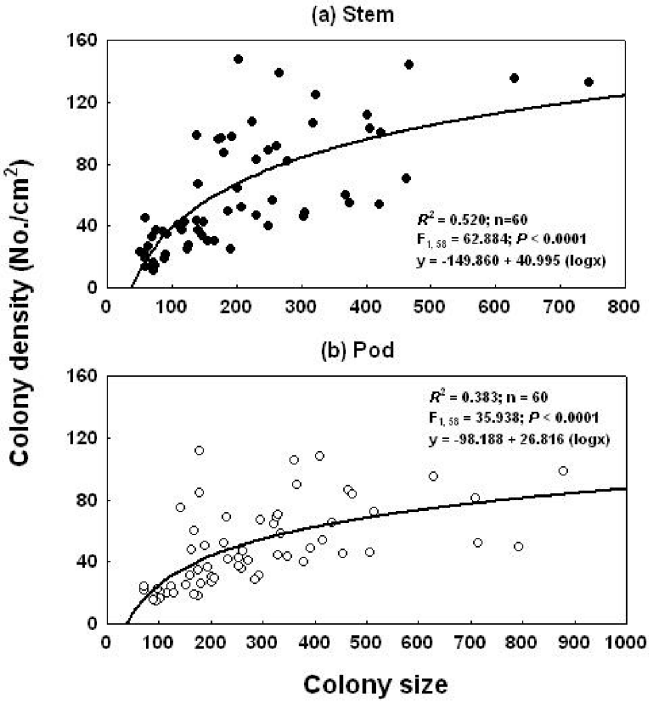

Fig. 3 *Aphis craccivora* colony density vs. log colony size linear relationship for *Vigna unguiculata* stem (a) and pod (b)

to optimize colonization of both stem and pod surface representing the food resource available. The significant positive correlations between colony area and colony size for stem and pod further supported the idea of optimal utilization of food resource. The lack of significance for colony size vs. colony length relationship in stem and colony size vs. colony circumference relationship in pod could be related to structural differences in the plant organs. While stems of a given age or position have more or less uniform circumference but are interspersed with leaves which break the linear colony contiguity, pods of any age display some variation in circumference yet provide uninterrupted linear dimension for colonization. The general negative colony density vs. colony dimension relationships pointed out that with increased availability of food resource, the aphid tended to spread out its colonies to avoid intra-specific competition and vice-versa. However, the positive correlation between colony density and colony size indicated that with a rise in population and consequent increase in colony size on resource units, i.e. stem and pod, the aphid showed a tendency to compact its colonies. The slightly better fit of linear-log relationship than the simple linear model between colony density and colony size suggested that density increases at a decreasing rate, probably mediated by reduced fecundity with colony growth (Way, 1968), and reaches an upper limit at saturation of the resource unit.

While significantly higher colony length, colony circumference and colony area in pod than in stem indicates that the aphid is more expansive on pod than on stem, governed probably by the contiguous surface area available in pod, significantly higher colony size in pod points out the possibility of preferential colonization. On the other hand, similar colony density in stem and pod seemed to suggest that the aphid does not require differential densities to overcome host defenses or utilize food from these two resource types representing source and sink, respectively. It is possible that during reproductive phase of the crop when stems and pods are available abundantly, the aphid exploits the two resource types equally by maintaining uniform densities on them.

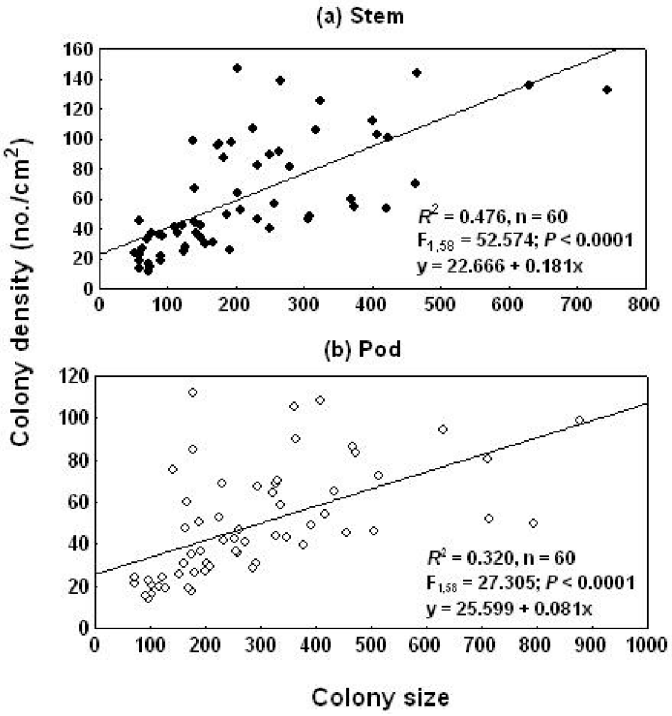

Fig. 4 *Aphis craccivora* colony density vs. colony size linear relationship for *Vigna unguiculata* stem (a) and pod (b)

Lack of skewness in colony density on leaflets of top most leaf and leaflets of top 2nd or 3rd leaf appears to be a case of finite resource size limiting proliferation of *A. craccivora*. Nevertheless, higher density on leaflets of top most leaf than on leaflets of top 2nd or 3rd leaf suggested some possibilities. For example, Ibbotson and Kennedy (1951) suggested that unequal distribution of *Aphis fabae* among leaves primarily reflected intrinsic differences between leaves, aided by gregariousness, whereas aggregation on leaves primarily reflected gregariousness and only secondarily differences between portions of the leaf. Within plants, leaf stage selection and colonization by aphids were related to differential leaf toughness and phloem phytochemistry, despite the possibility of higher concentrations of defensive metabolites in phloem sap of young leaves than in that of old leaves (Gould *et al.,* 2007; Jakobs *et al.,* 2019). Higher density of *A. craccivora* on top immature

Table 4. Comparative colony density statistics of *Aphis craccivora* on leaflets of top most leaf and leaflets of top 2nd or 3rd leaf in *Vigna unguiculata*

Resource type	Shapiro-Wilk W@	Skewness z#	Colony density (no./cm²)
Leaflets of top most leaf	0.956*	1.265ns	38.98 ± 19.63$ (9.0 - 81.0)
Leaflets of top 2nd or 3rd leaf	0.926**	1.565ns	19.35 ± 9.62 (6.25 - 38.75)
Mann-Whitney U test (Z# value)	-	-	5.76****

@ Shapiro-Wilk W: significance at $^{*}P < 0.05$; $^{**}P < 0.01$ # Skewness/SE of skewness; ns not significant ($z < \pm 1.96$) (Cramer and Howitt, 2004); $ Mean ± SD; n=60; Figures in parentheses are range; Significance at **** $P < 0.0001$

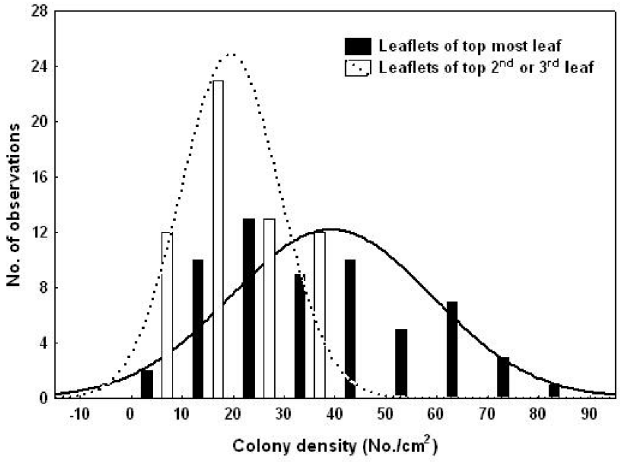

Fig. 5 Frequency distribution of *Aphis craccivora* colony density on leaflets of top most leaf and leaflets of top 2nd or 3rd leaf of *Vigna unguiculata*

leaves of *V. unguiculata* could be due to both nutritional suitability and lack of metabolites, besides the possible ability of the aphid to divert food from other leaves through phloem and acting somewhat like a sink (Way and Cammell, 1970).

The gradation of stem, pod, leaflets of top most leaf and leaflets of top 2nd or 3rd leaf in the decreasing order for *A. craccivora* colony density reinforced the trends observed in stem vs. pod and leaflets of top most leaf vs. leaflets of top 2nd or 3rd leaf comparisons. In earlier studies on alfalfa, higher proportions of *A. craccivora* (Berberet *et al.,* 2009) and *Acyrthosiphon kondoi* (Zarrabi *et al.,* 2005) were found on stems than on leaf blades. Similarly, populations were higher and aphid development period was shorter for *Aphis glycines* on stems than adaxial and abaxial leaf surfaces of soybean (Nalam *et al.,* 2021). Aggregations aid in overcoming host defenses and mobilizing or utilizing host nutrients (Prokopy, 1981; Sandström *et al.,* 2000), since aphids probe often and remain with their stylets inserted longer in the presence of colony members (Ibbotson and Kennedy, 1951). Variable aggregation size or colony density of *A. craccivora* in the four organs of *V. unguiculata* may be an adaptation to serve these two functions. If these organ-specific aggregations represent optimal densities, their ranges are likely to change with growth of aphid populations through different phenological stages of the host plant, as the positive correlations between colony size and colony density in stem and pod indicated.

Aphid species are known to be constrained chemically to certain plant species or even parts of the plants governed by chemical profile and trichome arrays (Loxdale *et al.,* 2019). Both between and within-plant differences in phloem sap chemistry are known to affect the performance and

Table 5. Comparison of *Aphis craccivora* colony density on different resource types in cow pea

Resource type	Colony density (no./cm^2)
Stem	61.10 (157.87)^a
Pod	49.45 (145.62)^{ab}
Leaflets of top most leaf	38.98 (122.70)^b
Leaflets of top 2nd or 3rd leaf	19.35 (55.82)^c

Figures in parentheses are mean rank values; Mean ranks followed by the same letter are not significantly different ($P > 0.05$) by multiple comparison, z values of Kruskal-Wallis test ($1/2^2 = 77.377$, df=3, n=240, $P < 0.001$)

abundance of aphids in relation to their nutritional needs, and behavioral or physiological responses (reviewed in Jakob *et al.,* 2019). Performance of *A. glycines* on a specific location of soybean plant is primarily driven by accessibility and the quality of phloem composition rather than structural traits (Nalam *et al.,* 2021). The preferential attack of different host plants (Srikanth and Lakkundi, 1988b) with differential rates of reproduction (Srikanth and Lakkundi, 1988c) by *A. craccivora* could be due to the relative suitability of hosts determined by morphological, anatomical, physiological and nutritional factors. On the other hand, among different organs of *V. unguiculata*, although higher colony dimensions and colony size of *A. craccivora* in pod (sink) than in stem (source) seem to support the idea of preferential colonization of these plant parts, similar colony density on these two organs appears to reject the possibility of different optimal densities. Systematic simulation studies to assess the fitness or reproductive performance of the aphid at different densities on the four organs, in relation to within-plant phytochemical composition (Enyiukwu *et al.,* 2018), would shed some light on the occurrence of optimal densities to either maximize nutrient utilization or overcome host defenses. Since optimal densities are likely to change with crop growth and the consequent aphid population buildup, such studies need to be carried out at different phenological stages of the crop to reveal their temporal dynamics.

From applied ecology point of view, within-plant variation in colonization pattern of *A. craccivora* has implications for sampling accuracy. Based on the concentration of a high percentage of the aphid population in the middle and lower portions of alfalfa canopy, Berberet *et al.* (2009) suggested sampling by removal of stems for accurate population estimate. Differential colonization rates in *V. unguiculata* in the present study indicated that sampling stems, leaflets of top most leaf and leaflets of top 2nd or 3rd leaf in the vegetative phase, and pods in the reproductive phase would be ideal for estimating *A. craccivora* populations in studies on population dynamics of the aphid and natural enemies (Srikanth and Lakkundi, 1990).

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