

Gall distribution as a compromise between the optimal gall-site selection and the synchrony to host-plant phenology in the aphid *Kaltenbachiella japonica*

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Abstract Gall-site selection by the aphid *Kaltenbachiella japonica* was evaluated in relation to leaf position in a shoot, and gall positions within a leaf. First-instar fundatrices induce closed galls on the midribs of host leaves, and several galls were often induced on one leaf. Leaves with many galls were often withered before emergence of sexuparae from the galls. Within a leaf, gall volume was positively correlated with the sum of lateral-vein length in the leaf segment at which the gall was induced. The observed pattern in gall volume among the leaf segments corresponded with that in the lateral-vein length. These results show that a foundatrix selects the most vigorous position within a leaf to produce more offspring. Although distal leaves grew faster than did basal leaves, gall density was highest on leaves at the middle order when a shoot has more than seven leaves. Optimal gall-site selection seems to be constrained by the asynchrony in timing between the hatching of fundatrices and leaf growth within a shoot. These results suggest that the observed gall distribution is affected by both the distribution of suitable galling sites within a leaf and the synchrony with leaf phenology of the host plant.

Keywords Plant vigor hypothesis · Synchronization hypothesis · Herbivore · Gall-site choice

Introduction

Gall-inducing insects stimulate the leaves, buds or stems of the host plant to promote the proliferation of the tissues from which the larvae take nutrients (Price et al. 1987; Hartley and Lawton 1992; Stone and Schönrogge 2003; Allison and Schultz 2005; Suzuki et al. 2009). The nutritional quality of galls varies markedly among the positions where galls are induced, even within an individual plant (Feeny 1970; Whitham 1978; Scriber and Slansky 1981; Craig et al. 1989; Akimoto and Yamaguchi 1994; Cornelissen et al. 2008). These observations suggest that the gall position within a host plant directly affects the fitness of the gall inducer and, consequently, that gall inducers that choose suitable gall sites will be selected for. Previous studies have identified two factors that influence gall-site selection. First, the plant vigor hypothesis (PVH; Price 1991) postulates that herbivorous insects will preferentially attack vigorously growing position of a plant because of the nutritional advantages associated with such behavior. Several studies have tested the PVH in gall-inducing insects such as aphids, sawflies and cynipid wasps (Kimberling et al. 1990; Price 1991; Hartley 1998; Price and Price 2000; Fritz et al. 2000, 2003; Rehill and Schultz 2002, 2003; Koyama et al. 2004; Cornelissen et al. 2008). Second, the ability of gall inducers to synchronize with plant phenology is considered to have a significant effect on the success of gall induction (Crawley and Akhteruzzaman 1988; Weis et al. 1988; Komatsu and Akimoto 1993; Tikkanen et al. 1999; Yukawa 2000; Wool 2004; Mopper 2005; Imai and Ohsaki 2009). In galling aphids that

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overwinter as eggs, the first instars (fundatrices) need to select suitable galling site and begin inducing a gall immediately after setting on the site. As in the larvae of sessile scale insects, the fundatrices are unable to search for optimal galling sites for an extended period or over long distances (Itioka and Inoue 1991). In addition, since the temporal window of the host plant for gall induction is very narrow, the synchronization of aphid hatching with the leafing out of the host plant is crucial in determining the spatial distribution of galls and, consequently, in characterizing the preference–performance relationship in gall-inducing aphids (Dixon 1976; Yukawa 2000). Given these temporal constraints, it has been hypothesized that gall distribution is affected by the extent to which aphid egg hatching is synchronized with host leafing (synchronization hypothesis, SH; Akimoto and Yamaguchi 1994). Consequently, a gall inducer may not choose the optimal site from the viewpoint of plant vigor because of physiological constraints in response to the host phenology.

The fitness of a fundatrix may also be affected by the position of the gall on a leaf. Galls at a more basal position on a leaf blade absorb relatively more nutrients from the whole leaf and even from adjacent leaves (Larson and Whitham 1991). Thus, when several *Pemphigus betae* galls coexist on the same *Populus* leaf, the most basal galls exhibit the highest fecundity and survival (Whitham 1978). However, in other gall-inducing aphids, the fundatrix fitness is highest when the gall is induced in the midsection of the leaf (for *Neothoracaphis yanonis*; Ngakan and Yukawa 1996; for *Dinipponaphis autumnata*; Ngakan and Yukawa 1997) or at the apical position of the leaf (Akimoto and Yamaguchi 1994). The selected gall-inducing position may vary depending on the leaf position to which the largest amount of nutrients is transferred.

Certain aphid species are able to modify the organization of plant vascular system tissues to increase food supply (Wool et al. 1999; Wool 2004). In the galling aphid *P. betae*, the size of galled leaves is correlated with the survival, fecundity and body mass of the fundatrices in the galls; there is a tendency among fundatrices to colonize larger leaves (Whitham 1978). Variation in performance (e.g., fecundity or survival rate) associated with galling sites has been examined in another gall-inducing aphid, *N. yanonis* (Ngakan and Yukawa 1996). While these studies support the PVH, the correlation between aphid performance and galling sites has not been observed in other species of galling aphids (Burststein and Wool 1993; Akimoto and Yamaguchi 1994; Ngakan and Yukawa 1997). When simultaneous adaptations to several host-plant traits are constrained, gall distribution would be realized as a compromise between optimal gall-site selection and adaptation to host-plant phenology. However, no previous studies have considered the combined action of

both plant vigor and the synchrony with growth of the host plant.

In the present study, gall-site selection by fundatrices is investigated in the aphid, *K. japonica* Matsumura, which induces completely closed galls on the midribs of the leaves of *Ulmus davidiana* var. *japonica*. First, we tested the PVH within a leaf and investigated whether larger galls contain more offspring or not, and then, we examined the correlation between the gall volume and total lengths of lateral vein within leaf segments on which the gall is induced. On the basis of these data, we examined a hypothesis that a foundatrix selects the most vigorous position within a leaf. Second, we investigated the relationship between growth rate of leaves within a shoot and number of induced galls on each leaf. From the PVH, a foundatrix should select the leaf showing the highest growth rate. On the basis of the results, we show that gall-site selection by fundatrices is affected by multiple selection factors that cannot be optimized simultaneously.

Materials and methods

Aphids and study site

Kaltenbachiella japonica is a gall-inducing aphid associated with the Japanese elm, *U. davidiana* var. *japonica*. The aphid has a non-host alternating life cycle, which means that it remains on the same host-plant species for the entire year (Akimoto 1985). In early spring, fundatrices hatch from overwintered eggs on the trunk of *U. davidiana* from where they walk to growing leaves. The first-instar fundatrix then settles along the lateral side of the midrib on the underside of a growing leaf and pricks the area where the midrib abuts the leaf tissue. The site stimulated in this way swells over time to form a globular gall on the midrib of the upper side of the leaf. Such galls reach their maximum size in mid-July. While the final size and the number of the parthenogenetically produced aphid offspring vary between galls, approximately 100–200 such offspring are produced per gall. These offspring develop into sexuparae (winged forms with sexual females and males). From late July to mid-August, sexuparae emerge from the ruptured galls and walk to the stem of the same host tree. Upon reaching the stem, the sexuparae produce apterous males and females (sexuales), which mature without feeding and mate approximately 1 week after birth. Each sexual female then lays a single egg in a crevice of the bark in early August, and the eggs hatch in the following spring (Akimoto 1985). Two Japanese elm trees on the campus of Hokkaido University in Sapporo, northern Japan (43°03'N, 141°21'E), were selected for this study. The trees were mature (>10 m tall) and harbored numerous galls induced

by *K. japonica*. Galls of other aphid species, for example, *Tetraneura* spp., were also found on these trees.

Growth rate and final size of leaves

In order to clarify the relationships between aphid traits (gall distribution and fundatrix fecundity) and plant traits (growth rate and final leaf size), we estimated the growth rates of developing leaves from spring to summer in 2006. In this study, we refer to a current-year shoot that has grown from a single bud (see Fig. 1). On 16 May 2006, branches with growing shoots (mid-May) were randomly collected from the two trees and preserved in a freezer ($-20\text{ }^{\circ}\text{C}$) until the measurements were taken. To remove the effects of galls on leaf growth, only shoots without galls were selected for the measurements of this stage. The measured traits of shoots are summarized in Fig. 1. Then, in late May, early July and September, the leaf measurements were repeated to estimate the growth rate of leaves. In each period, we measured each 20 leaves for each leaf order. Briefly, the growth rate of leaves was calculated by subtracting the length of leaves at late May from those at September. Mid-May, late May, early July and September corresponded, respectively, to when the buds of the tree burst, the fundatrices hatched, galls matured and sexuparae emerged.

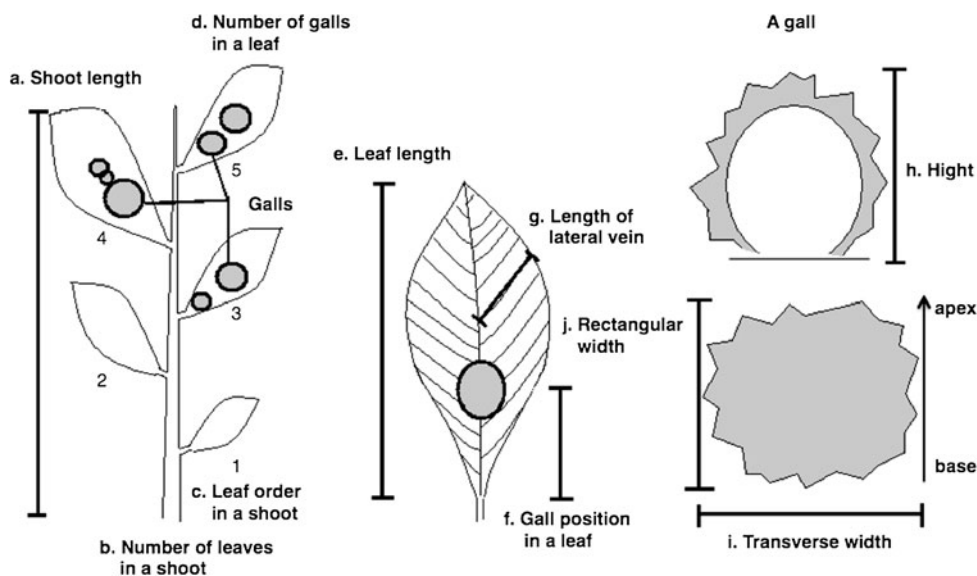
In order to estimate the effect of leaf shape on the performance of fundatrices, we measured the lengths of the lateral veins (see Fig. 1) at each measurement period. To accurately specify the position of a gall on a leaf, the midribs of leaves were divided into ten equal segments (0–9). In each segment, the length of the longest lateral vein on each side of a leaf was measured and summed to obtain an index of nutrient flow in each segment.

Gall size and number of offspring within a gall

We investigated the relationship between gall size and number of offspring produced in the gall. From late July to early August 2005, a total of 197 (90 and 107 from each tree) mature galls (judged by their brownish color) were collected together with leaves and preserved in 80 % ethanol. Gall height (in Fig. 1h) was measured as the distance from the bottom to the top of a gall on the upper surface of the leaf. We used two indices to infer gall width; “transverse width” (in Fig. 1i) is the maximal gall width orthogonal to the leaf midrib, and “longitudinal width” (in Fig. 1j) is the maximal length of a gall along the midrib. These indices were measured to 0.01 mm for every collected leaf using a vernier micrometer. Gall volume was calculated as an approximation to an elliptic sphere using the equation, $4/3\pi \times i/2 \times j/2 \times h/2$. After the measurements had been taken, the galls were dissected and the number of offspring in each gall was counted. To remove the effect of competition among galls, examinations were restricted to leaves with only one gall.

The relationship between the variables describing gall location and gall size was then examined to elucidate the most suitable site for gall induction. For this comparison, a branch that had not been used for previous collections was selected in each tree. For all the galls in these branches, we recorded the following variables: “shoot length” (in Fig. 1a), “the number of leaves on a shoot (leaf number),” “leaf position on a shoot from the base of the shoot (leaf order),” “leaf length” and “gall position on a leaf.” These variables were recorded in the field from late June to mid-August in 2005. The position of each gall was calculated as the distance of the gall site from the leaf base relative to the leaf length. After the measurements were taken, gall

Fig. 1 Plant characteristics measured in this study



volume was calculated by the method presented above. As a result, the above five variables and the gall volume were obtained for each gall.

A multiple regression analysis was then performed to assess the effect of each the five variables on gall volume. Because a preliminary study showed that gall volume was highest at the midpoint of the longitudinal midrib axis, we considered a second-order term of gall position in the regression model. The model with the squared gall position was compared with the model without the second-order term using Akaike's information criterion (AIC). To facilitate interpretation of the results, only leaves with a single gall were used in the analysis.

We also examined the gall-site preference of fundatrices among and within leaves, and the number of galls for each leaf order category was also counted for shoots with different leaf numbers. Gall-site preference within a leaf was evaluated by counting the number of galls in each leaf segment. To show the gall-site preference of all fundatrices, we included aborted galls in these analyses. Gall abortion occurs when galls fail to develop due to the death of the fundatrix.

Results

Leaf characters determining gall volume

In total, 1,645 galls were used in this analysis. AIC criteria selected a multiple regression model with the second-order term (squared gall position). The results are summarized in Table 1. After the backward stepwise selection of variables, three factors (gall position within a leaf, squared gall position and leaf order) were selected as significant variables that affected gall volume (Table 1). Thus, we concentrated on gall position and leaf order in the subsequent analyses. When all the other variables than the gall position were fixed as constants, we obtained a second-order curve ($Y = -6,028.48X^2 + 4,003.14X$). This concave curve had a peak at $X = 0.33$, indicating that the best position for a gall is expected in the third leaf segment.

Vein length and gall volume in leaf segments

A total of 30 leaves were analyzed for lateral-vein length. In each leaf segment category (0–9), no significant differences were observed between the longest lateral veins on each side (t test, $p > 0.05$ for all segments). We therefore used the sum of the two lateral-vein lengths as an index of vein length in a segment. The vein length increased to segment 3 and then decreased to apical segments (Fig. 2). One-way ANOVA with a post hoc test showed that although the differences are not significant among segments 2–4, these 3 segments have significantly longer veins than the other segments. This means that the vein length has a peak at ca. 1/3 position from the leaf base.

A total of 269 leaves having a single gall were used to analyze the relationship between gall volume and number of offspring. Gall volume ranged from 59.2 to 1,367.4 mm³, with an average volume of 526.1 mm³. The average number of offspring per gall was 146.4, ranging from 31 to 301. Since a positive correlation was observed between gall volume and the number of offspring ($r = 0.678$, $n = 269$, $p < 0.0001$), gall volume was used as an index of fitness of a fundatrix in subsequent analyses.

There were 114, 90, 45, 13, 7 and 1 galls in the 0, 1, 2, 3, 4 and 6 segments, respectively. Fig. 3 shows the distribution of gall volume to the relative position within a leaf. The second-order regression (the curved line in Fig. 3) indicated that gall distribution also has a peak at ca. 1/3 position from the leaf base. Average gall volumes in leaf segment are presented in Fig. 2. There is a significant difference in the gall volumes among the segments (one-way ANOVA, $F = 10.36$, $df = 4$, $p < 0.0001$). Both the vein length and the gall volume have a similar trend (increase to the segment 3 and decrease from there), but differences among the segments 2–4 were not statistically significant (a post hoc test by Tukey-Kramer's method). However, the average gall volume in the segment 0 was significantly smaller than that in the other segments. These results indicate that the gall volume has a convex distribution. In addition, a significant positive correlation was

Table 1 Multiple regression data for the effect of morphometrical factors on gall volume

Factors	Partial regression coefficient	SE	Standardized partial regression coefficient	t	p	Standardized partial regression coefficient after the stepwise selection
Shoot length	28.26	10.21	0.417	2.770	0.0060	Not selected
Leaf number in a shoot	-84.58	28.67	-0.479	-2.950	0.0035	Not selected
Leaf order	74.72	27.41	0.208	2.727	0.0068	0.157
Leaf length	2.80	1.85	0.099	1.513	0.1314	Not selected
Gall position in a leaf	3,935.55	768.98	0.760	5.118	<0.0001	0.821
Squared gall position	-5,931.99	1,594.50	-0.548	-3.720	0.0002	0.590

Variables remaining after stepwise selection are also shown

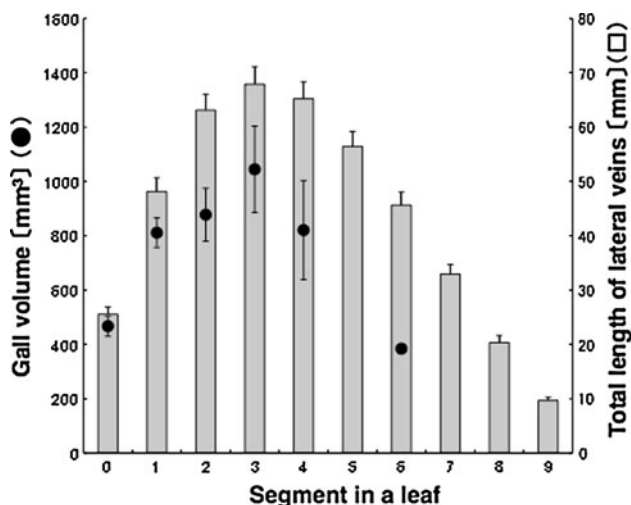


Fig. 2 Average gall volume and total length of lateral veins in each leaf segment. A squared-bar represents total vein length in each leaf segment. A closed circle shows average gall volume on a segment. Bars indicate SE

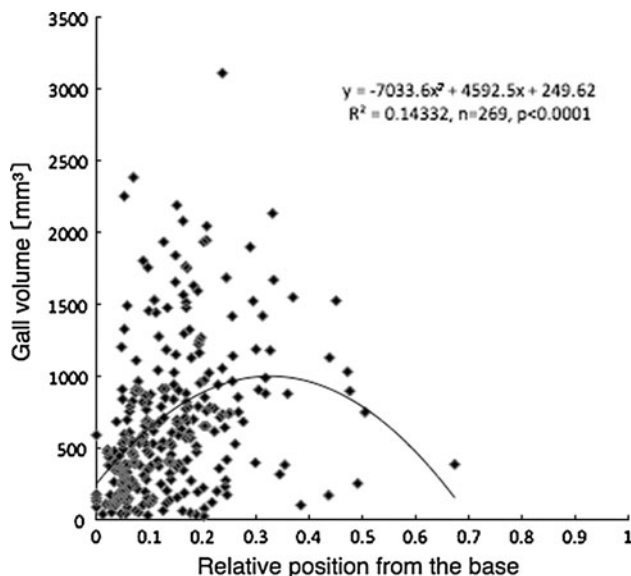


Fig. 3 Relationship between relative gall position within a leaf and gall volume. The curve is the second-order regression. The regression equation is also shown

detected between the vein lengths and the gall volumes among the segments ($\rho = 0.410$, $z = 6.732$, $p < 0.001$, Spearman's rank correlation). Thus, the foundatrices that induced her gall at positions having long veins succeeded to obtain larger galls and subsequent high fitness.

Growth rate of leaves within a shoot

Although we used leaves without galls in this growth rate analysis, it should be noticed that, when more than 3 galls were induced on a leaf, most of them (45/48) have been aborted before the emergence of sexuparae. Most of the

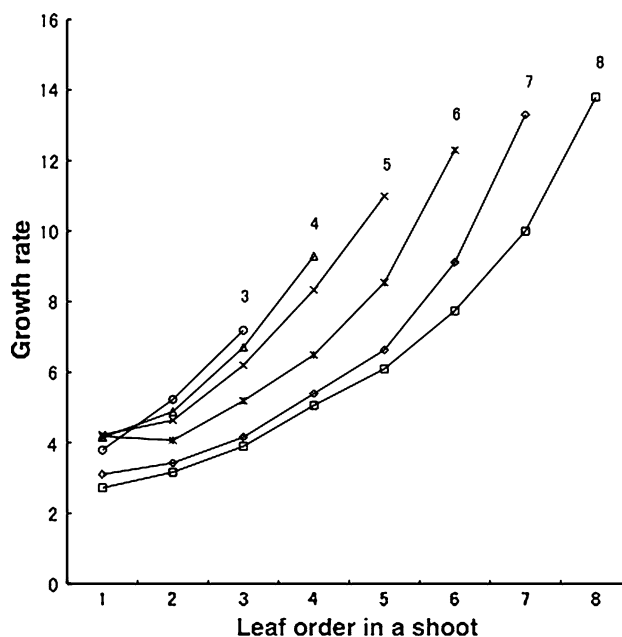


Fig. 4 Growth rate between mid-May and September for each leaf order in shoots having different numbers of leaves. Growth rate increase to apical leaves in each category

shoots on the trees examined had three to eight leaves, and we restricted our analysis to such shoots. Leaf length for each leaf order category did not differ between early July and September (t test, $p > 0.05$ for all pairs), implying that leaves have finished growing by early July. Growth rate until September was higher for apical leaves than for basal leaves (Fig. 4), indicating that apical leaves are more vigorous than basal leaves.

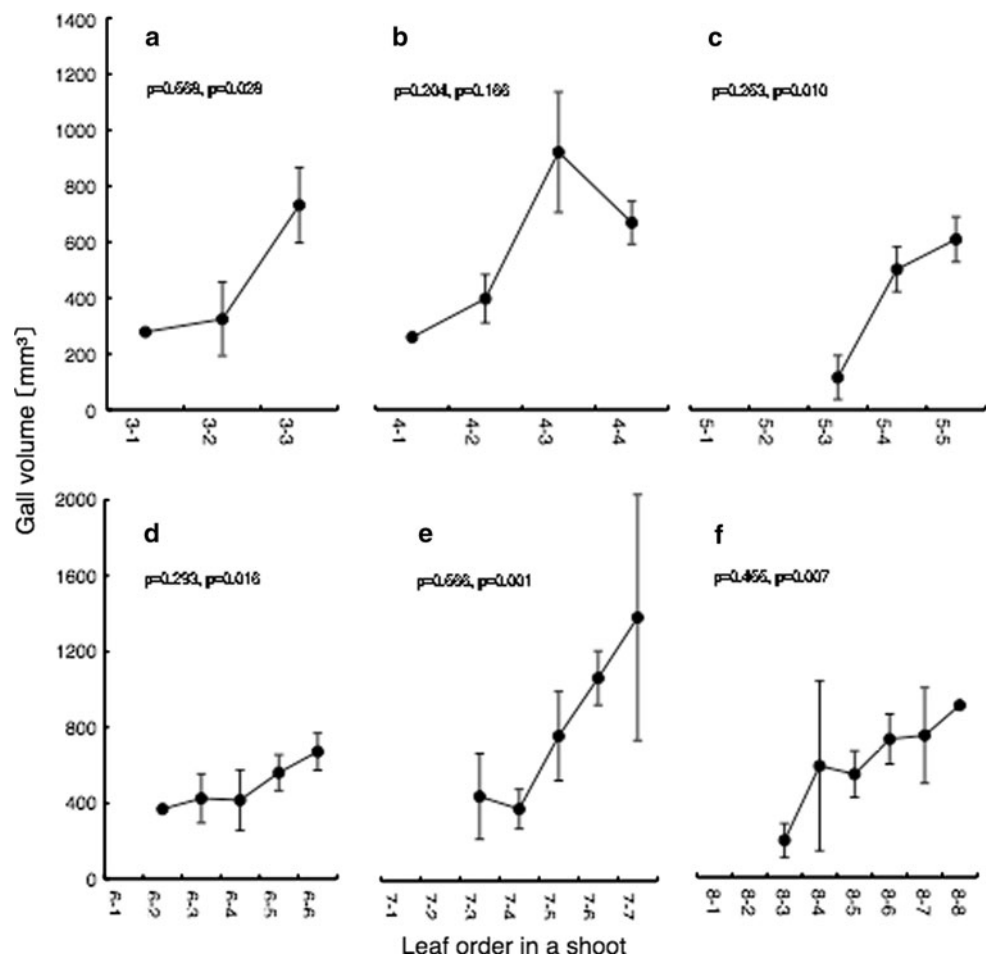
Relationships between shoot characteristics and gall volume

Effects of leaf order and leaf number on gall volume were analyzed for 193 shoots. Except for shoots with four leaves, rank correlation analyses indicated that there are significant positive correlations between leaf order and gall volume (Fig. 5a–f). This result indicates that gall volumes were larger in apical leaves. Conversely, the average gall volume did not vary among shoots with different leaf numbers (one-way ANOVA, $F = 2.25$, $df = 6$, $p = 0.26$). In conclusion, gall volume was affected by leaf order but was not affected by leaf number in a shoot.

Gall distribution among leaves on a shoot

For the analysis of gall distribution among leaves on a shoot, we investigated 3,124 galls on 389 shoots from the two trees (876 and 2,248 galls, respectively). The number

Fig. 5 Average gall volume on the leaves of shoots with different numbers of leaves. The average and SE are shown. For each shoot category for leaf number, a rank correlation coefficient is shown with the statistical probability. Other than the shoot with 4 leaves, gall volume increases to apical leaves



of galls varied significantly among leaf orders for any shoot category ($p < 0.001$ for all the shoot categories, one-way ANOVA). The number of galls increased with leaf order in shoots with fewer than seven leaves (Fig. 6a–d; $p < 0.001$ for all the categories, Spearman's rank correlation). However, the distribution of gall number has a convex shape in shoots with seven or more leaves (Fig. 6e, f). For both the categories, post hoc tests showed that the distribution has a peak at middle-ordered leaves. These results imply that fundatrices selected more distal leaves on shoots with six or fewer leaves and that, on shoot with more than six leaves, the fundatrices could not reach to distal leaves that have higher growth rates (see Fig. 4).

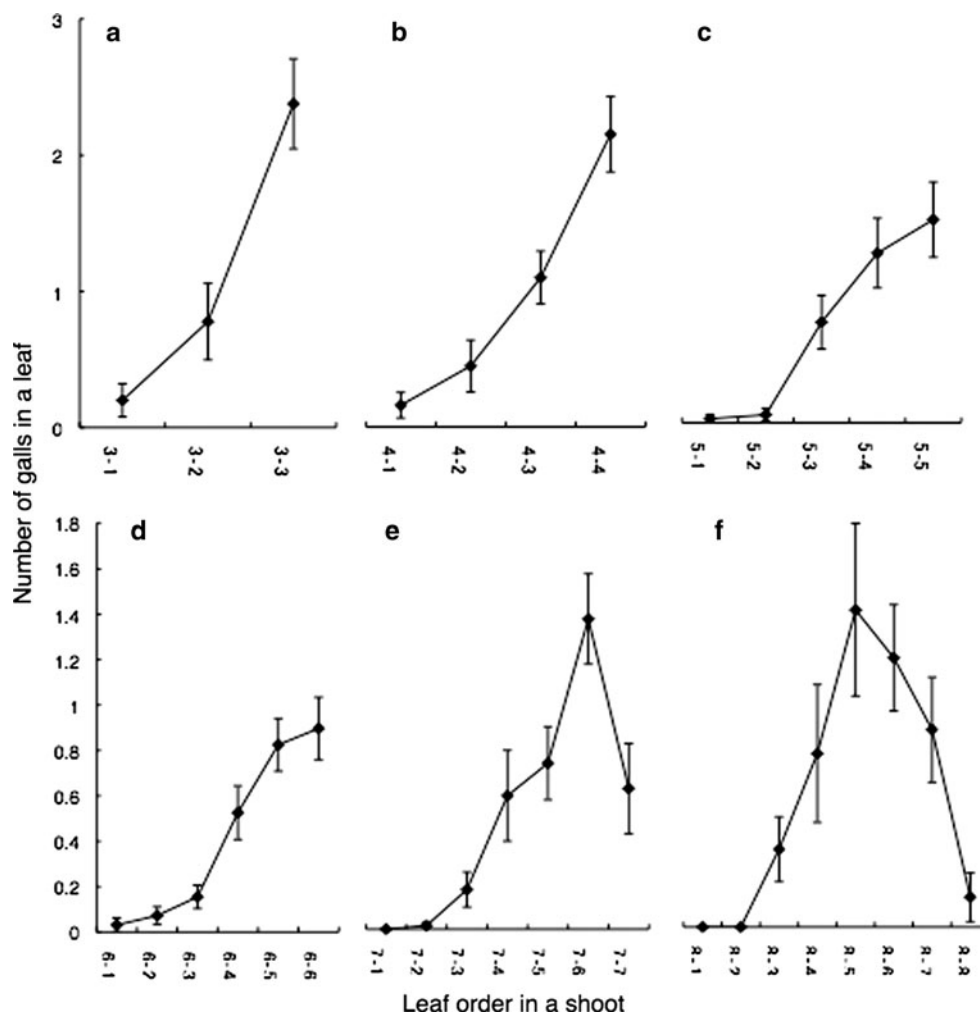
Discussion

The present study found that the number of *K. japonica* offspring produced in a gall was positively correlated to gall volume, corroborating observations in other aphids (*N. yanonis* (Ngakan and Yukawa 1996), *D. autumnna* (Ngakan and Yukawa 1997), *Hormaphis hamamelidis*

(Rehill and Schultz 2001) and implying that gall volume can be used as an index of fundatrix fitness. Larger galls can absorb more nutrients from the surrounding leaves (Larson and Whitham 1991, 1997; Burstein et al. 1994) and may provide larvae with a larger inner surface from which more offspring can feed. Since a suitable galling site would enable a fundatrix to induce a large gall, selection of such a site can have a marked effect on her fitness (Whitham 1978).

Although a positive correlation was observed between the gall volume and the leaf order, gall volume was not affected by the final leaf length (Table 1). Leaf order was positively correlated with leaf growth rate (Fig. 4), and it is likely that the rapid growth of distal leaves facilitated the vigorous growth of galls on their surface, irrespective of the final leaf size. There are several evidences indicating that larger galls function as sinks for photosynthesized compounds and amino acids (Whitham 1980; Larson and Whitham 1991; Inbar et al. 1995). Fay and Whitham (1990) reported that galls on vigorously growing shoots facilitated high reproductive outputs and growth rates in the aphid offspring supported by those galls. In

Fig. 6 Average gall number on leaves of shoots with different leaf numbers. Gall number increases to apical leaves in the shoots with 3–6 leaves. The gall number distributions are convex shaped in the shoots with more than 6 leaves



K. japonica, larger galls contained more offspring, suggesting that a fundatrix can obtain higher fitness when she selected more vigorously growing sites of the host plant.

Within a leaf, gall volume was statistically larger in middle segments where the vein lengths were also long (Fig. 2). Similar results are reported in the galling aphids, *N. yanonis* and *D. autumnna*; in these species, the performance of the fundatrices was greatest at the particular position within a leaf (Ngakan and Yukawa 1996, 1997). Galls of the aphid *P. betae* showed the highest performance at the most basal position of leaves where the lateral veins were longest (Whitham 1978; Larson and Whitham 1991). Since galled leaves continue to photosynthesize as the gall grows (Larson and Whitham 1991; Inbar et al. 1995), lateral veins may serve as a pathway of photosynthetic products that are transported from the peripheral leaf areas to the leaf midrib. Thus, although the position of the longest lateral veins may vary among host-plant species, galls located at the base of the longer lateral veins may acquire more nourishment than galls at other locations of the leaf surface. The selection of such optimal sites on the leaf would

facilitate the development of larger galls and increase fundatrix fitness. Although we could not statistically determine the optimal segment in the used segmentation, this is not a problem for our conclusion. Since the post hoc tests indicated a convex shape of the distribution, we can derive the optimal segment from the same data by using a more coarse segmentation. The important fact is the observed correspondence between distribution of the vein length and that of gall volume. In fact, gall volume was positively correlated with the vein length, indicating the optimal site selection within a leaf by *K. japonica* fundatrices.

While number of galls increased with leaf order in shoots with fewer leaves than seven, this relationship was not observed on shoots with seven or more leaves (Fig. 6). This is interesting because the distal leaves on the later shoots had larger growth rates (Fig. 4), suggesting favorable conditions for galling at these leaves. The discrepancy between this potential condition and the observed gall distribution can be explained if the apical leaves on longer shoots start growing later than those on shorter shoots. Most of the first instars would fail to access the apical

leaves of long shoots. This may be possible because leaves start growing from the basal to the apical positions on shoots, which means that the apical leaves of long shoot will start to develop later than the apical leaves of shorter shoots. Thus, selection of an optimal galling site by fundatrices may be constrained by the asynchrony that exists between the time of egg hatching and the leafing time of hosts. The mean hatching time of overwintered eggs of *K. japonica* is closely synchronized with the mean budding time of host trees; nevertheless, considerable variation in hatching time exists among eggs collected from a single tree (Komatsu and Akimoto 1993). Although the time window during which fundatrices can induce galls is highly restricted (Akimoto 1998), the differences in hatching time among fundatrices would result in a large variation in the timing of gall induction. Thus, the observed variation in hatching time would lead to galls being more widely distributed on trees, decreasing the competition among fundatrices for optimal galling sites. In fact, most leaves with multiple galls have been withered before the emergence of sexuparae. Thus, the realized pattern of gall distribution may be affected by a combination of factors, including gall-site selection by fundatrices, variation in egg hatching time, competition among fundatrices and temporal variation in optimal leaves. While most previous studies have focused on one of these factors to consider gall position or distribution, this study emphasizes the need to consider the simultaneous action of possible selective factors when considering gall distribution patterns in gall-inducing insects.

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