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ORIGINAL ARTICLE

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Invasive *Eupatorium adenophorum* suffers lower enemy impact on carbon assimilation than native congeners

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Abstract Enemy release hypothesis predicts that alien plants that escape from their natural enemies suffer lower enemy regulation in their introduced ranges than in native ranges. An extension of this theory suggests that if enemy release plays a crucial role in invasive success, then in the introduced range, invasive plants should also suffer lower local enemy impact than native residents (local enemy release hypothesis, LERH). In order to test LERH, we compared invasive *Eupatorium adenophorum* with two native congeners (*E. heterophyllum* and *E. japonicum*) in terms of damage by leaf enemies at two natural field sites and two manipulated sites. We also determined enemy impact on carbon assimilation at two manipulated sites. In each site, *E. adenophorum* was only damaged by herbivores, while in native congeners, leaf scabs or (and) leaf rolls was found in addition to herbivory damage. In both manipulated sites, the total enemy impact on carbon assimilation was lower for *E. adenophorum* than for native congeners; this observation was consistent with LERH. The results of this study indicate that a short co-existence time with generalist enemies (behavior constraint) might be the main contributor to the lower enemy impact on *E. adenophorum*.

Keywords Invasive · Herbivory · Scab · Roll · Behavior constraint · Enemy impact

Introduction

Biological invasion is a potential threat to biodiversity and has been a focus of ecological research. Invasive plants usually grow aggressively and adversely affect the ecosystem and socioeconomic development (Mack et al. 2000; D'Antonio and Kark 2002; Pimentel 2002). Identifying the factors that contribute to invasive success is very important for predicting and controlling potentially invasive plants. However, the mechanisms underlying invasiveness are still not well elucidated (Levine et al. 2003).

The enemy release hypothesis (ERH) is an important theory that explains alien plant invasions. ERH posits that alien plants introduced into a new region escape from their natural enemies, resulting in an increase in distribution and abundance (Keane and Crawley 2002). The success of several classical biological agents provides evidence for ERH (Van Driesche and Bellows 1996; McFadyen 1998). Biogeographical studies have been conducted to test ERH directly (Dewalt et al. 2004; Reinhart et al. 2010). However, in the introduced range, comparing enemy impact between invader and native species is also critical in order to test the role of enemy release on invasive success (Agrawal et al. 2005). Consequently, we proposed the local enemy release hypothesis (LERH). According to this hypothesis, invasive plants suffer lower enemy impact than native species in the introduced range, giving the invader a competitive advantage. Several community studies have proven that invasive plants suffer less enemy damage from herbivores, parasites, and/or pathogens than native plants (Agrawal et al. 2005; Carpenter and Cappuccino

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2005), although some studies have reported inconsistent patterns (Gross et al. 2001; Colautti et al. 2004).

In the introduced range, comparing local enemy impact between invasive species and native congeners is a more rigorous way of testing LERH than by using other species. Alien species that are related to native species are more likely to acquire enemies from among those that threaten the native species (Andow and Imura 1994; Agrawal et al. 2005; Dawson et al. 2009). Funk and Throop (2010) surveyed 19 pairs of taxonomically related invasive and native species in Hawaii and found that the native species showed higher leaf-damage rates than the invasive species. There are several gaps in the findings of previous studies regarding the role of enemy release. Most studies have only focused on enemy diversity, abundance, and damage level, and have not considered the relationship between enemy damage and growth (Hierro et al. 2005). Different types of enemy damage have different impacts on plant growth. Further, various species might also respond differently to the same damage. Moreover, most studies are conducted in one site alone, even though some studies have shown that for the same species, enemy damage might differ among sites (Siemann and Rogers 2003; Dietz et al. 2004).

Several factors can affect enemy preference, such as leaf toughness, nutrient quality, and volatile organic compounds. Behavioral constraints also play an important role in enemy preference, especially for alien plants. Agrawal et al. (2005) found that although alien invasive plants had weaker resistance to enemies than native congeners, they still suffered less enemy damage than native species. This lower resistance might be due to the short coexistence time between alien invasive plants and local enemies. Avoiding novel plants can help generalist insects reduce the risk of feeding on toxic plants (Abrahamson and Weis 1997; Lankau et al. 2004).

Eupatorium adenophorum (also known as *Ageratina adenophora* (Sprengel) R. M. King and H. Robinson), originating from Central America, is an invasive perennial shrub found worldwide. It can infest diverse habitats such as roadsides, grasslands, croplands, woodlands, and limestone shrubs, causing great damage to the biodiversity and structure and function of the invaded ecosystems (Tian et al. 2007). A lot of work has been done to investigate the invasiveness of *E. adenophorum*. Niu et al. (2007) found that *E. adenophorum* can alter the soil community in a way that favors itself and inhibits native species. Our pervious study showed that *E. adenophorum* has more ramets and higher leaf area than native species (Zheng et al. 2009). In another study, we found that *E. adenophorum* has evolved so as to increase nitrogen allocation to photosynthesis (growth) and reduce allocation to cell walls, resulting in higher height and poorer structural defenses than native conspecifics (Feng et al. 2009). However, until now, no study has been performed to test LERH for *E. adenophorum*. In native ranges, there are more than 30 phytophagous insect species and additional pathogens for *E. adenophorum* (Fritz Heystek, pers. comm.), and in introduced ranges, *E. adenophorum* was also attacked by some insects (Yadav and Tripathi 1985; pers. obs.). In order to test whether *E. adenophorum* was released from local enemies, we compared leaf damage by enemies in *E. adenophorum* and two native congeners (*Eupatorium heterophyllum* and *Eupatorium japonicum*) at two natural field sites and two manipulated sites. We also examined consumption differences of two generalist insects between leaves of *E. adenophorum* and native congeners by performing a feeding experiment in the laboratory. Next, we determined the impact of damage on carbon assimilation and explored the potential reasons for any differences in enemy impact between *E. adenophorum* and native congeners in the manipulated sites. We hypothesized the following: (1) local enemies have a lower impact on *E. adenophorum* than on native congeners, and (2) behavior constraints contributed to lower enemy impact on *E. adenophorum*.

Materials and methods

Species and study site

E. adenophorum spread into Yunnan Province in the 1940s from Burma. Now, it has invaded six provinces in southwestern China and continues to invade northern and eastern China. It replaces native species and even forms a dense monoculture in many habitats. *E. japonicum* and *E. heterophyllum*, native to many provinces in China, occur in many habitats, including the understory and edge of forests, shrubs, and grasslands. All invasive and native species are perennial forbs that are 1–2 m in height.

Enemy damage was investigated at two natural field sites (Zhujiashan and Xishan) and two manipulated sites (located in Qujing Normal College), while the enemy impact on carbon assimilation was determined only in the manipulated sites. Zhujiashan (25°19′N, 102°56′E, 2,100 m a.s.l.) is around Kunming, Yunnan Province, Southwest China. The vegetation was a secondary forest. Xishan (25°02′N, 102°39′E, 2,350 m a.s.l.) is about 40 km away from Zhujiashan. *E. japonicum* has sympatric distributions with *E. adenophorum* in Zhujiashan (hereafter ZS), while *E. heterophyllum* co-occurred with *E. adenophorum* in Xishan (hereafter XS).

Qujing Normal College (25°31′N, 103°45′E, 1,877 m a.s.l.) is about 135 km away from Kunming and included two sites: one site (hereafter QO) was open and received sunshine, while the other (hereafter QS) was a shade house (with 36 % irradiance). The shade house had steel frames covered with one layer of black nylon shade netting. The lower 40 cm of the shade house remained open to facilitate herbivore movement and air flow. Seedlings of *E. adenophorum*, *E. japonicum*, and

E. heterophyllum were planted in both sites. Seeds of each species were collected from ZS and XS. These seeds were then sown in a seedbed of QS in July 2007. In September, when the seedlings of the three species were approximately 10 cm in height, similar-sized seedlings were transplanted singly into 8-dm^3 pottery pots. The pots were filled with a top layer of mountain soil (70 %) and river sand (30 %). All seedlings were grown in the shade house for 2 weeks. Then, the seedlings of each species were randomly divided into two groups, and each group was grown in QO and QS.

Measurements

Evaluation of enemy damage

In August 2008, in the two field sites, we first randomly sampled a plot (15 × 15 m) in each site. Then, 15 individuals of each species were randomly chosen from each plot in order to detect leaf damage. In the two manipulated sites, 25 random individuals were selected in order to detect leaf damage in each species. The leaf damage was divided into three categories: herbivory (leaf partially eaten by herbivores), scab (leaf has some scab because of pathogens), and roll (leaf was rolled because of some microorganisms, herbivores, or spiders, etc.). We measured leaf herbivory as the percentage of the number of leaves that had been damaged (herbivory) and the percentage of leaf area that had been consumed by herbivores (loss area). Leaf scab and leaf roll were calculated as the percentage of the number of leaves that showed scabs and rolling, respectively. If the same leaf had more than one type of damage, we classified it on the basis of which damage has the greatest impact on carbon assimilation.

Feeding choice experiment

In September 2009, we studied the feeding choice of two generalist herbivores (*Helicoverpa armigera* Hübner and *Spodoptera litura* Fabricius) with regard to *E. adenophorum* and native congeners. In the field, we observed that *H. armigera* and *S. litura* ate *E. japonicum* and *E. heterophyllum* but not *E. adenophorum*. The herbivores were presented with two food options; this meant that each culture dish had a leaf of *E. adenophorum* and *E. japonicum* (or *E. adenophorum* and *E. heterophyllum*). This experiment was performed in the laboratory at room temperature and in the presence of scattering light. Before the experiment, the larvae of the two herbivores were not fed for 12 h, and then they were put in culture dishes with pairs of leaves (*E. adenophorum* and *E. japonicum* or *E. adenophorum* and *E. heterophyllum*), such that there was one larva in one culture dish. For each food combination, there were eight replicates. After 60 h, we determined the leaf area that was consumed (consumption area) and calculated the percentage of each leaf area that was consumed (consumption fraction).

Determination of the rate of photosynthesis

In both sites of the Qujing Normal College, the light-saturated photosynthetic rate ($P_{\max}$) of healthy and damaged leaves were measured for five individuals of each species. For each individual, one leaf of each kind (healthy and damage categories) was selected for analysis. The $P_{\max}$ was measured in the morning by using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA) under saturating level of photosynthetic photon flux density (PPFD, 2,000 μmol m^{-2} s^{-1} for individuals grown under 100 % irradiance and 1,500 μmol m^{-2} s^{-1} for individuals grown under 36 % irradiance). The relative humidity and CO$_2$ concentration in the air in the reference chamber were controlled at 60 % and 380 μmol mol^{-1}, respectively, and the leaf temperature was maintained at 20 °C. Before measurements, each sample leaf was illuminated with the saturating level of PPFD for about 10 min in order to achieve full photosynthetic induction. For each kind of leaf, if possible, the center part was used to determine $P_{\max}$. For herbivory leaves, if the remaining part was not big enough for the leaf chamber of Li-6400, the $P_{\max}$ was calculated again according to the actual leaf area in the leaf chamber. For scab leaves, the part for analysis had many scabs. For rolled leaves, the leaves were first unrolled and then examined.

Calculation of enemy impact

For each sample, we assumed that if the damaged leaves did not suffer herbivory, scab, and roll damage, their $P_{\max}$ was equal to that of healthy leaves. We also assumed that the loss area (the part of the leaf consumed by herbivores) had the same $P_{\max}$ as the healthy leaves. For each sample, we defined the loss area as A_{loss} and the remaining total leaf area as $A_{\text{remaining}}$. A_{healthy}, $A_{\text{herbivory}}$, A_{scab}, and A_{roll} represent the area of herbivory, scab, and roll damage, respectively. Thus, the total leaf area was $A_{\text{total}} = A_{\text{loss}} + A_{\text{remaining}}$, and $A_{\text{remaining}} = A_{\text{healthy}} + A_{\text{herbivory}} + A_{\text{scab}} + A_{\text{roll}}$. P_{healthy}, $P_{\text{herbivory}}$, P_{scab}, and P_{roll} were $P_{\max}$ values for healthy, herbivory, scab, and roll leaves, respectively. The enemy impact on growth was evaluated as the percentage reduction in photosynthetic production accumulation. The enemy impact for each category was calculated as follows:

$$\text{Herbivory impact} = \left[P_{\text{healthy}} \times A_{\text{loss}} + \left(P_{\text{healthy}} - P_{\text{herbivory}}\right) \times A_{\text{herbivory}}\right] / \left(P_{\text{healthy}} \times A_{\text{total}}\right) \quad (1)$$

$$\text{Scab impact} = \left[\left(P_{\text{healthy}} - P_{\text{scab}}\right) \times A_{\text{scab}}\right] / \left(P_{\text{healthy}} \times A_{\text{total}}\right) \quad (2)$$

$$\text{Roll impact} = \left[\left(P_{\text{healthy}} - P_{\text{roll}}\right) \times A_{\text{roll}}\right] / \left(P_{\text{healthy}} \times A_{\text{total}}\right) \quad (3)$$

For each species, the total enemy impact was the sum of the above types of enemy impact.

Statistical analyses

For each variable, one-way analysis of variance (ANOVA) (for three groups) or *t* test (for two groups) was used to test the differences among the species at the same site. We also used one-way ANOVA or *t* test to test the differences in the types of enemy impact among the species at each site. The *t* test was used to test the differences in consumption area (and consumption fraction) between *E. adenophorum* and native species for each food combination. All analyses were performed using SPSS 12.0 (SPSS Inc., Chicago, IL, USA).

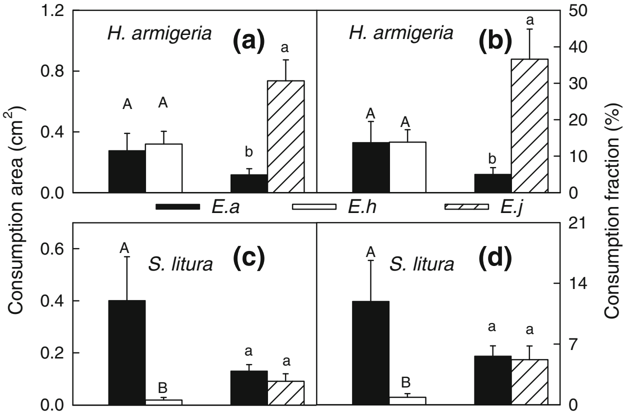

Fig. 1 Consumption area and consumption fraction of *Helicoverpa armigera* and *Spodoptera litura* for *E. adenophorum* (*black bars*), *E. japonicum* (*open bars*), and *E. heterophyllum* (*hatched bars*). Different *capital letters* indicate significant differences between *E. adenophorum* and *E. japonicum*; different *lowercase letters* indicate significant differences between *E. adenophorum* and *E. heterophyllum* ($p < 0.05$)

Results

In each site, *E. adenophorum* was only damaged by herbivores, while *E. japonicum* showed scabs in addition to damage by herbivores (Table 1). *E. heterophyllum* was damaged by herbivores at all sites, but it only showed scabs at QS and QO and rolling at QS (Table 1).

Herbivore damage to *E. adenophorum* was significantly higher than that to *E. japonicum* and *E. heterophyllum* at QO and significantly higher than that to *E. japonicum* at QS (Table 1). However, the loss area was not higher for *E. adenophorum* than for native congeners at both sites (Table 1). At XS and ZS, both herbivore damage and loss area were significantly lower in *E. adenophorum* than in the two congeners (Table 1).

In terms of consumption area and consumption fraction of *H. armigera*, there were no significant differences between *E. adenophorum* and *E. heterophyllum* (Fig. 1a, b); however, these values were significantly lower for *E. adenophorum* than for *E. japonicum* (Fig. 1a, b). In terms of consumption area and consumption fraction of *S. litura*, there were no significant differences between *E. adenophorum* and *E. japonicum* (Fig. 1c, d); however, these values were significantly higher for *E. adenophorum* than for *E. heterophyllum* (Fig. 1c, d).

There were no significant differences in terms of impact of herbivore damage between *E. adenophorum* and *E. japonicum* at QO and QS. However, the impact of herbivore damage on *E. heterophyllum* was significantly lower than that on the previously mentioned plants (Fig. 2a, b). Except for *E. japonicum* at QS, both native congeners showed scabs, and this type of damage was significantly more than the damage caused by herbivores (Fig. 2a, b). For *E. japonicum* at QS, rolling damage was significantly higher than the damage caused by herbivores and not significantly different from scab damage (Fig. 2b). The total enemy impact was significantly greater for native congeners than for *E. adenophorum* at QO and QS (Fig. 2c, d).

Discussion

As predicted by LERH, the invasive *E. adenophorum* suffered lower total enemy impact than the native congeners (Fig. 2c, d). In all sites, only herbivory damage was found in *E. adenophorum* (Table 1). However,

Table 1 The differences in herbivory, loss area, and scab among the invasive *Eupatorium adenophorum* and its native congeners at each site, according to one-way analysis of variance (Duncan's test) or *t* test

Categories	Site:	Xishan		Zhujiashan		Qujing open site			Qujing shade house		
	Species:	*E. a*	*E. h*	*E. a*	*E. j*	*E. a*	*E. h*	*E. j*	*E. a*	*E. h*	*E. j*
Herbivory (%)		10.6b	21.7a	18.9b	30.2a	28.0a	7.34c	18.8b	26.6a	11.2b	21.3a
Loss area (%)		0.26b	2.79a	0.31b	1.80a	1.93b	0.82b	4.18a	1.72ab	1.33b	3.5a
Scab (%)		0	22.6	0	0	0	45.2a	27.6b	0	43.2a	43.8a
Roll (%)		0	0	0	0	0	0	0	0	0	23.7

Species mean values were given for each enemy category. Different *letters* indicate significant differences among species for each enemy category at each site

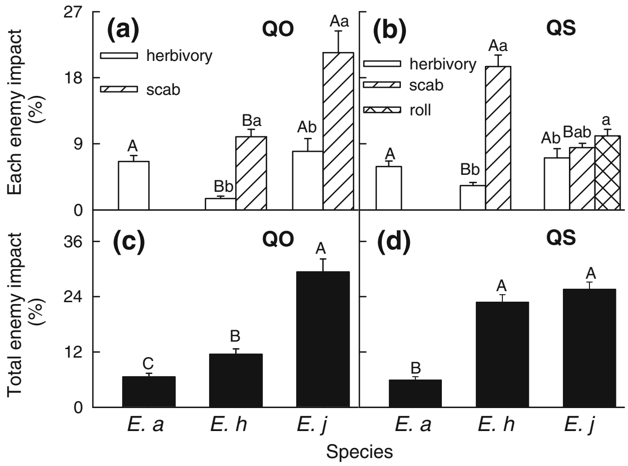

Fig. 2 Each enemy (herbivory, scab, and roll damage) and total enemy impacts on *E. adenophorum* and the native congeners. Different *capital letters* indicate that for each impact, there were significant differences among the species; different *lowercases* indicate that for each species, there were significant differences among the different impacts ($p < 0.05$)

besides herbivory damage, the two native species also suffered scab damage, and *E. japonicum* also suffered roll damage at QS (Table 1). Other studies have also found that invasive plants suffer lower levels of enemy damage than native species in introduced ranges (e.g., Dietz et al. 2004; Agrawal et al. 2005; Carpenter and Cappuccino 2005).

In the field, the two generalist herbivores (*H. armigera* and *S. litura*) did not feed on *E. adenophorum*. However, in the feeding choice experiment, for most food combinations, the consumption area and consumption fraction were not lower for *E. adenophorum* than for the native congeners (Fig. 1). These results were consistent with the behavioral constraint hypothesis. Agrawal et al. (2005) also found that invasive plants had weaker resistance to enemies than native congeners, even while suffering less enemy damage than native species. Our results suggest that *E. adenophorum* was considered edible by *H. armigera* and *S. litura*; however, they did not recognize it as a suitable food source under natural conditions. This result might be attributable to the short co-existence time for *E. adenophorum* and local enemies. Avoiding novel plants can help the generalist insects reduce the risk of feeding on toxic plants (Abrahamson and Weis 1997; Lankau et al. 2004).

Previous studies have found a strong site-specificity for herbivore damage in invasive species (Prieur-Richard et al. 2002; Dietz et al. 2004). They considered that plant community diversity, abundance, and structure differed among sites and that species-rich communities support greater herbivore diversity. This may lead to high herbivore damage in invasive species (Prieur-Richard et al. 2002; Dietz et al. 2004). However, in this study, the higher herbivore damage in *E. adenophorum* at QO and QS (Table 1) was not attributable to the rich community at both sites. Both sites were located in the university, and the plant community diversity and abundance were much lower than those in ZS (secondary forest) and XS (limestone shrub). The higher herbivore damage in *E. adenophorum* might be related to an alteration in the feeding behavior of some generalist herbivores. The feeding behavior of generalists is often plastic, and host choice can be altered by environmental factors (Bernays and Chapman 1994; Lankau et al. 2004). In Qujing, *Acrydium japonicum* Bolivar (Orthoptera: Tettigidae), *Agriolimax* sp. (Stylommatophore: Agriolimacidae), *Callimorpha albipuncta* Wileman (Lepidoptera: Arctidae), a species of *Limacodidae* (Lepidoptera), a species of *Tortricidae* (Lepidoptera), and a species of *Geometridae* (Lepidoptera) attacked *E. adenophorum*. However, they never fed on *E. adenophorum* in the field. There is a big nursery (about 5,000 m^2) near the Qujing experiment sites, and pesticides and fungicides were applied regularly at these sites. However, we did not use pesticides or fungicides in this study. Consequently, the food choices for some herbivores were reduced, and some generalists that usually do not attack *E. adenophorum* might have been forced to incorporate it in their diet. After some time, generalists might have recognized *E. adenophorum* as a suitable food source, leading to higher herbivory damage and loss area in *E. adenophorum*. This result is evidence for behavior constraints of generalist enemies in terms of their feeding on *E. adenophorum* in natural environments.

Herbivory damage can not only affect plants directly by depleting photosynthetic leaf tissue but can also indirectly reduce photosynthesis in the remaining parts of the leaves (Zangerl et al. 2002; Aldea et al. 2005). Occasionally, the indirect effect is greater than the direct effect (Zangerl et al. 2002; Aldea et al. 2006). However, to the best of our knowledge, we are the first to quantify differences in carbon assimilation in invasive versus resident native species, with respect to both direct (loss area) and indirect herbivory effects (photosynthesis reduction in the remaining part) (see enemy impact calculation, Eq. 1).

In the present study, there were no significant differences in $P_{\max}$ between *E. adenophorum* and the native congeners (Fig. 3 in Appendix). However, the total leaf enemy impact was significantly lower for *E. adenophorum* (Fig. 2c, d); this means that under equivalent conditions, *E. adenophorum* could accumulate more photosynthetic product and have a competitive advantage over the native species. In this study, we only detected leaf enemy damage, and further studies are required to compare the effects of other damage (to the root and stem) by other potential enemies between *E. adenophorum* and the native congeners. Two previous studies have shown that there was a positive soil feedback for *E. adenophorum* in China (Yu et al. 2005; Niu et al. 2007). In order to test the role of enemy release more precisely in the *E. adenophorum* invasion process, enemy exclusion (including aboveground and belowground enemies) experiments between native and invasive ranges need to be performed. In summary, the

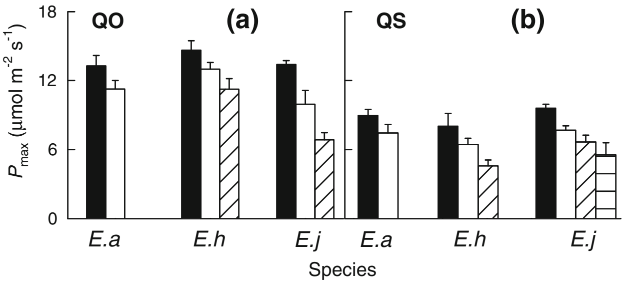

Fig. 3 P_{max} for healthy leaves (*black bars*), leaves with herbivory damage (*open bars*), leaves with scab damage (*bars* with *diagonal lines*), and leaves with roll damage (*bars* with *horizontal lines*) for each species at Qujing open site (*QO*) and Qujing shade site (*QS*)

results of our study support LERH, and invasive *E. adenophorum* suffered lower leaf enemy impact than two native congeners. Further, the results of this study indicate that in natural environments, the lower damage suffered by *E. adenophorum* might be mainly attributable to the behavioral constraints of some generalist enemies.

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Appendix A

See Fig. 3

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