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Risk assessment for non-crop hosts of Pea Enation Mosaic Virus and the aphid vector Acyrthosiphon pisum

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1   **Abstract**

2   Viral insect-borne plant pathogens have devastating impacts in agroecosystems. Vector-borne

3   pathogens are often transmitted by generalist insects that move between non-crop (weedy) and

4   crop hosts. Insect vectors can have wide diet breadths, but it is often unknown which hosts serve

5   as pathogen reservoirs and whether vector abundance in non-crop hosts is predictive of outbreaks

6   in crops. We addressed these issues by linking field surveys of an aphid vector and plant virus

7   with statistical models to develop risk assessments for legume crops. In the Pacific Northwest

8   USA, the pea aphid (*Acyrthosiphon pisum*) is a key virus vector with a wide host range; in 2018

9   we completed a 65-site survey where aphids were surveyed in weedy legumes within and outside

10   dry pea fields. We quantified the abundance of pea aphids on seventeen hosts, and plant tissue

11   was tested for *Pea enation mosaic virus* (PEMV), a pathogen that causes considerable yield

12   losses in certain years. High densities of *A. pisum* were found exclusively in habitats dominated

13   by hairy vetch (*Vicia villosa*), which was the only legume other than cultivated pulses where

14   PEMV was detected. Our results indicate that *V. villosa* is a key alternative host for PEMV, and

15   that pest management practices in this region should consider the distribution and abundance of

16   this weedy host in viral disease mitigation efforts for legume crops.

17

18   **Keywords:** Aphids, legumes, plant viruses, reservoirs, non-crop hosts

19 **Introduction**

20 Plant viruses cause an average 10% reduction in global agricultural productivity, which

21 translates to global economic losses of more than US $30 billion annually (Strange & Scott 2005,

22 Jones 2021). Most crop plant viruses require insects for transmission, especially phloem-feeding

23 Hemipterans like aphids (Power 2000; Hogenhout et al. 2008). However, despite the importance

24 of vector-borne plant viruses in agriculture, our ability to predict virus occurrence across time

25 and space remains poor for most pathosystems. Many vectors are generalists with a broad host

26 range that includes food and cover crops, agricultural weeds, and native plants (Mueller et al.

27 2012, Bommarco et al. 2007). Identifying host reservoirs is key to determine the source(s) of

28 vector-borne pathogens that can outbreak in a crop system (Peterson 2018, Gobatto et al. 2019).

29 Like their vectors, many crop viruses occupy alternative hosts before infecting crop plants

30 (Norris & Kogan 2005). Non-crop hosts have been established as reservoirs for insect vectors

31 and vector-borne pathogens that infect annual crops such as wheat, corn, and rice (Rashidi et al.

32 2020, Wu et al. 2020). The replication and spread of a plant virus across multiple hosts depends

33 on the compatibility and coordinated interactions of virus- and host-encoded proteins, and the

34 severity of infection often differs among hosts (Heinlein 2015, Basu et al. 2018). Assessing

35 whether certain hosts act as reservoirs of pathogens can be difficult, however, especially if

36 alternative hosts do not show clear signs of infection because many viruses can exhibit slower

37 replication in certain hosts by avoiding cellular damage (Lucas 2006, Takashi et al. 2019). Yet,

38 management strategies for crop pathogens rely on identifying the potential for non-crop hosts to

39 serve as pathogen reservoirs for vectors and pathogens using molecular diagnostics (Rageshwari

40 et al. 2017). Understanding how pathogens and vectors move among many potential plant hosts

41 patches is also an important component of effective management of crop diseases.

42   When a non-crop host for pathogens or vectors is identified, integrated pest management

43   (IPM) strategies suggest targeted removal to prevent crop infection (Catton et al. 2015, Macharia

44   et al. 2016). For example, management of wheat stem rust relies on control of the pathogen's

45   alternative host American barberry, a strategy that dates back almost a century (Peterson 2018).

46   Non-crop host removal can be difficult if these host plants are also weeds, however, particularly

47   those that emerge early in seasons before crops are established (Norris & Kogan 2005).

48   Consequently, some agricultural weeds allow pest insect populations to increase before moving

49   into crops, exacerbating outbreaks of herbivores themselves in crops. Colorado potato beetle is

50   observed feeding on horse nettle before moving into potato (Mena-Covarrubias et al. 1996), and

51   two spotted spider mites disperse from weeds to cotton (Wilson 1995, Norris & Kogan 2005).

52   Movement of generalist vectors between non-crop and crop hosts can mediate the spread of

53   pathogens (Power et al. 1991; Davis et al. 2015; Srinivasan et al. 2008). Aphids that migrate over

54   long distances often establish population in crops rapidly in the spring months as non-crop hosts

55   senesce, which is often accompanied by high prevalence of virus-infected plants (Clement et al.

56   2010, Reynolds et al. 2006). Aphids with long-distance dispersal capability as alates can also

57   complicate management efforts (Damgaard et al. 2020, Powell et al. 2006, Mueller et al. 2012).

58   For these reasons, aphid-borne viruses are hard to track and outbreaks are often unpredictable,

59   hampering pest management (Damgaard et al 2019). To address such challenges, identification

60   of local sources of aphid-borne pathogens can be of great value in guiding optimal and cost-

61   effective control strategies, such as removal of weedy reservoirs near crop fields. In turn, the

62   goal of our study was to track and quantify potential non-crop hosts for a problematic pathogen

63   and its vector in a single region (eastern Washington state and Northern Idaho, USA).

64

Methods

Study System

The pea aphid *Acyrthosiphon pisum* is a frequent pest of pulse crops that acts as the main vector for several pathogens, including *Pea enation mosaic virus* (PEMV) (Rashed et al. 2018; Chatzivassiliou 2021). In addition to pea (*Pisum sativum*), PEMV infects crops and weeds like alfalfa (*Medicago sativa* L.), yellow sweet clover (*Melilotus officinalis* (L.), white sweet clover (*Melilotus albus* L.), wild white clover (*Trifolium repens* L.) common vetch (*Vicia sativa* L.), hairy vetch (*Vicia villosa* Roth), and broadbean (*Vicia faba* L.) (McEwen et al. 1957). Pea aphids acquire PEMV from a few perennial legume hosts and agricultural weeds (Hull 1981). However, *A. pisum* diet-breadth encompasses most of the Fabaceae (Peccoud et al. 2009), suggesting the diversity of PEMV-compatible hosts could be large. Plants infected with PEMV are stunted with malformed pods and ultimately have reduced yield (Clement et al. 2010). Extreme outbreaks can lead to up to 40% yield loss in pulses (Elbakidze et al. 2011, Paudel et al. 2018).

Survey Design

We conducted field surveys from May to July 2018 during an outbreak season of *A. pisum*. Pea aphids and virus have been monitored in eastern Washington and Idaho by the University of Idaho using a long-term trapping network for 17 sequential growing seasons. The 2018 season had the second highest alate arrival counts on a per-trap basis over this entire period (Fig. S1). This so-called "outbreak year" thus provided an opportunity to discover the non-crop hosts for *A. pisum* and PEMV in a season when aphids are widespread. Plant and aphid communities were sampled in two climatic ecoregions: Palouse Prairie, a high-elevation grassland predominately converted to dryland wheat production (Looney and Eigenbrode, 2012) and shrub-steppe, a

88   habitat found at lower elevations and warm slopes adjacent to the Palouse region (predominately

89   along the Snake River in Washington and Idaho) (Knick & Rotenberry 1997). Both habitat types

90   harbor a diverse community of herbaceous legumes and are purported sources of pea aphid

91   outbreaks (Clement 2006). All non-agricultural sites were in either roadside edges, native prairie,

92   or shrub-steppe. Agricultural sites were spring-planted pea fields on the lower Palouse in

93   Whitman Co. Washington and Latah Co. Idaho between 47.46°N and 46.33°N (Fig. 1).

94   Aphid, plant, and virus surveys were conducted using a line-transect (Fig S2). At each site

95   we ran 10 m line transects and quantified plant diversity (species identity) of all forbs touching

96   the line transect; forb percent cover was calculated by measuring the length of the line transect

97   (in cm) covered by plant material. At each transect we collected canopy arthropods using two

98   180° sweeps through the foliage; insects collected were stored in 95% ethanol until identification

99   to species. Samples of aboveground terminal leaf tissue of legume species overlapping the meter-

100   line transect were harvested, wrapped in aluminum foil, frozen in liquid N_2, and held on dry ice

101   before storing at -80°C. These tissue samples were used to determine the presence of PEMV.

102

PEMV detection in plants

104   To test all crop and non-crop legumes for PEMV, we used a two-stage protocol (Sint et al.

105   2016). First, we tested for PEMV by using reverse transcription-polymerase chain reaction (RT-

106   PCR) from pooled samples of all tissue collected from each transect (n = 65). Subsamples of

107   tissue from each plant, regardless of species, were pooled and ground into fine powder under

108   liquid N_2 by mortar and pestle into a transect-wide mix. Second, if PEMV was detected in the

109   pooled sample, the remaining tissue from all host plants was tested individually. This method

110 allows efficient scoring of each of plant in a sample for the presence PEMV while avoiding

111 unnecessary and costly sampling of individual plants if the entire population is free of the virus.

112   For detection of PEMV from plant tissue samples, 100 mg of homogenized tissue was run

113 through Promega SV total RNA isolation kits (Promega), producing cDNA from 1 µg of total

114 RNA using Bio-Rad iScript cDNA synthesis kits (Lee et al. 2021). Then RT-PCR was performed

115 using PEMV-1 coat protein specific primers (PEMV CP FP: 5' GTGGTGGCACCCTCTATG

116 3'; PEMV CP RP: 5' GTGTCCACATGGTAGGCTATG 3'). Primers were designed using the

117 IDT Primer Quest Tool for RT-PCR reaction (10 µl) containing 3 µl of ddH2O, 5 µl of dream

118 Taq mastermix (Thermo Scientific, Waltham, MA, usa), 1 µl of diluted primer mix (forward and

119 reverse [concentration 10µM]), and 1 µl of cDNA template. The RT-PCR program included an

120 initial denaturation for 5 min at 95°C followed by 21 cycles of denaturation at 95°C for 30 s,

121 annealing for 30 s at 56°C, and extension for 45 s at 72°C and final extension of 10 min at 72°C.

122 After PCR was complete, agarose gels (1%) were run at 90 v for 45 min, after which gel pictures

123 were taken in a documentation system (Bio-Rad, Hercules, CA). For one large population of

124 hairy vetch that contained PEMV (Fig. 1), we revisited the site later in the season and sampled

125 vetch plants in disturbed habitat fragments nearby. We verified that PEMV was present in an

126 adjacent habitat in a population of hairy vetch <1 km from the site at which PEMV was found.

127

128 ***Statistical Analyses***

129   All data analyses were completed using R version 4.1.2 (R Development Core Team 2021)

130 using base functions unless otherwise specified. For analyses of plant and aphid data, we used

131 GLMM (generalized linear mixed models) applying the 'lme4' package (Bates et al. 2015);

132 model estimates and P-values were extracted using the 'car' package (Fox and Weisberg 2011).

133   For plotting results and posthoc tests, we used the 'emmeans' package (Lenth 2016). Aphid

134   counts, or cumulative abundance models used a negative-binomial link function appropriate for

135   zero-inflated count data. Statistical analyses for line transects used site as a random effect.

136   Analyses of pooled long-term monitoring data from https://www.legumevirusproject.org/ were

137   completed using a GLMM with a negative binomial link function. These source data were

138   comprised of samples from a minimum of 30 pan traps monitored weekly over 17-year survey

139   period (Fig S1).

140

141   **Results**

142   We completed 118 transects at 65 sites, and opportunistically surveyed an additional five

143   hairy vetch populations. We collected 15,289 aphids in total and assayed 1,076 candidate plant

144   tissue samples for PEMV. In our transects we recorded 145 species of annual plants, of which 23

145   were in the family Fabaceae. We observed significant variation in the percent coverage of non-

146   crop legumes (Fig. 2) and the abundance of aphids among host plant species (Fig. 3).

147   Hairy vetch had the highest abundance of pea aphids and was the most abundant non-crop,

148   weedy legume (Fig. 3). At the community level, increasing coverage of vetch in transects was

149   related to a greater likelihood of pea aphid presence (GLMMs, $\chi^2 = 15.02$, $P < 0.0001$, Fig. 4).

150   Notably, adjacent habitats (N = x) also had high populations of hairy vetch colonized by pea

151   aphids upon subsequent revisit dates (Fig. S3). Finally, PEMV was only detected in hairy vetch

152   (Fig. S4) and crop (dry pea) sites colonized by pea aphids, but not in other hosts.

153

154

155

156 **Discussion**

157   Effective prediction of viral plant pathogen outbreaks requires a detailed understanding of

158 vector and pathogen movement from crop to non-crop hosts at the landscape scale (Srinivasan et

159 al. 2008). A first step in this process is risk assessment using potential alternative hosts (Holt et

160 al. 2008). Hairy vetch appears to be an ideal alternative host for pea aphids and PEMV, which

161 are major constraints on pulse production in the Palouse region of Pacific Northwestern US. We

162 found this host has high densities in non-agricultural environments, persists in disturbed habitats,

163 is correlated with aphid presence, and is validated as a competent host for PEMV.

164   Our understanding of pea aphid and PEMV outbreaks in the Palouse considers that pea

165 aphids likely colonize Palouse agroecosystems following wind currents from the Columbia Basin

166 and Willamette Valley, where milder winters allow aphids to overwinter on alfalfa and clover

167 (Clement et al. 2010, Hampton 1983). Genetic data shows that the pea aphid biotype found on

168 dry pea in the Palouse has shared markers with biotypes collected in these areas (Eigenbrode et

169 al. 2016). Our study suggests two possibilities that align with this information. First, hairy vetch,

170 which emerges early and in low elevation areas that warm up early in the growing season, is an

171 effective "stopover" host for aphid alates dispersing from warmer western regions to the Palouse.

172 Second, hairy vetch occurs in relatively warm microhabitats along the edge of the Palouse and in

173 the lower elevations in the Columbia Basin, and aphids may overwinter in these areas. Vetch is a

174 facultative biennial with an above-ground rosette during ideal climatic conditions (Pokorny et al.

175 2020, Mischler et al. 2010), and may have a small second generation in mesic habitats in the fall

176 and winter (Clark personal observations). In either case, vetch may act as a short- (months) or

177 long-term (years) reservoir for aphids and PEMV, playing an important role in this pathosystem

178 at the landscape scale. In some years, PEMV-infected vetch may provide inoculum for arriving

179 aphids, contributing to more injurious infections associated with early infection (Paudel 2018). In

180 years when infectious aphids arrive later in the season, if they colonize vetch, the pathogen can

181 gain a foothold for possible infection of legume crops in the following growing season.

182 Once non-crop hosts for specific plant pathogens are discovered, management implications

183 arise. For pathogens with many hosts, reduction of non-crop plants could reducing the incidence

184 of that pathogen in crops (Peterson 2018, Strickland et al. 2020). In other systems, management

185 of weeds may reduce pest populations in crops (Norris & Kogan 2005). However, in many cases

186 removal of non-crop hosts may not be viable if they occur over large geographic regions or when

187 movement of pests between hosts occurs over long distances, so local control would not prevent

188 outbreaks. However, in our system it is unclear if a weed removal strategy is tenable. Hairy vetch

189 is planted as a cover crop for cattle forage (Golden et al. 2016), and this is why it persists at high

190 abundance even as feral populations on dry hillsides. Hairy vetch also improves soil nitrogen,

191 prevents erosion, and is not listed as a noxious weed (Pokorny et al. 2020, Mischler et al. 2010).

192 Our results suggest that in this region, cover cropping of hairy vetch may increase PEMV

193 outbreak risk in dry peas if in the same fields, but further work would be needed to verify this

194 within-field spread occurs. For example, pathogen testing could be used to indicate if local

195 infection risk and movement from vetch to pulse crops could occur at a single site.

196 The optimization of pathogen detection from field samples also depends on precision and

197 specificity of the procedure to ensure efficient and accurate detection of true positive samples

198 (Yazdkhasti et al. 2021). The use of more advanced molecular detection techniques, such as real

199 time-PCR with much lower detection threshold can be used to detect pathogens with low titer

200 (Rubio et al. 2020). Another key step toward improved pathogen detection is to maintain the

201 quality and integrity of field samples by following proper collection techniques. These

202 precautions effectively enhance detection efficiency of pathogens from field samples.

203   Given the differences in phenology of cultivated pulses and hairy vetch in the Palouse

204 region (vetch emerges and hosts aphids earlier in the season), this work implies an important tool

205 may be available to predict prevalence of PEMV. Greenhouse work has demonstrated that pea

206 aphid adults feeding on vetches with PEMV can then transmit these viral pathogens to banner

207 pea (Clark et al. 2019). Sampling hairy vetch for aphids and PEMV may be a way to indicate if

208 there are risks of large-scale, catastrophic outbreaks of PEMV likely to occur each year. While

209 we only have one season of data reported here, PEMV and aphid populations go through large

210 and difficult to predict population cycles. Consequently, it appears likely that if PEMV is found

211 in April or early May in many hairy vetch populations along the lower Palouse, it would portend

212 an areawide impact of PEMV in the growing season for pulse farmers. Similar strategies could

213 be employed in other non-crop and crop source-sink dynamics systems where the non-crop host

214 is a perennial plant that emerges earlier in the growing season.

215

216   **Conflict of Interest Statement**

217   The authors declare no conflicts of interest.

218

219   **Author Contribution**

220   REC, DWC, and SDE and conceived project design. REC and ECO completed surveys and data

221   analysis. REC and SB completed molecular assays. SDE provided long-term aphid trap data. All

222   authors wrote, edited, and approved the final manuscript.

223

224   **Data Availability Statement**

225   Upon acceptance of this manuscript all data will be made available through a publicly available

226   GitHub data and code repository by REC.

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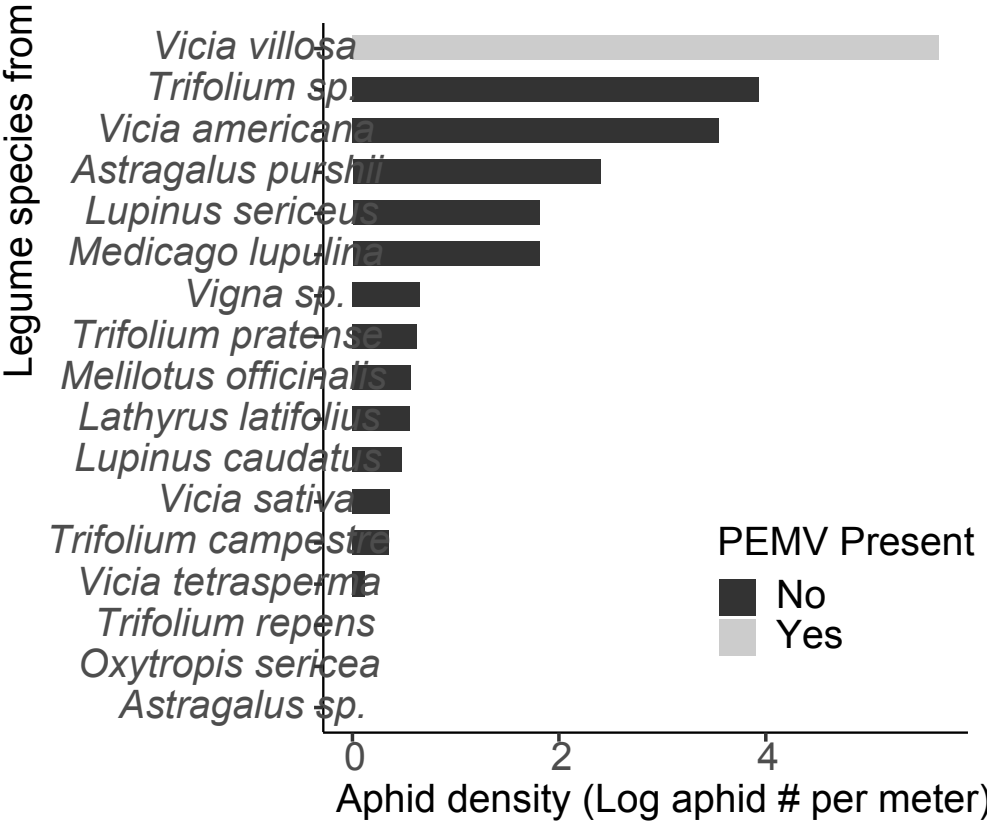
377   **Figure Legends**

378   Fig. 1. Sampling locations for crop and non-crop transects. All cultivated dry pea fields were

379   spring-planted fields in rotation with cereals. Non-agricultural sites included open public lands or

380   lands that gave permission to sample. Color indicates presence or absence of PEMV at a given

381   transect. The transects at Wawawai Canyon (westernmost non-agricultural site) yielded mixed

382   populations of infected and non-infected plant hosts.

383   Fig 2. Cumulative aphid density (log transformed) for legume hosts found among all surveys.

384   Bar colors indicate whether a host plant was discovered with PEMV RNA.

385   Fig. 3. Cumulative plant coverage for non-crop legumes found among all surveys; hairy vetch

386   was the most common. Bar length indicates the cumulative coverage among our sites.
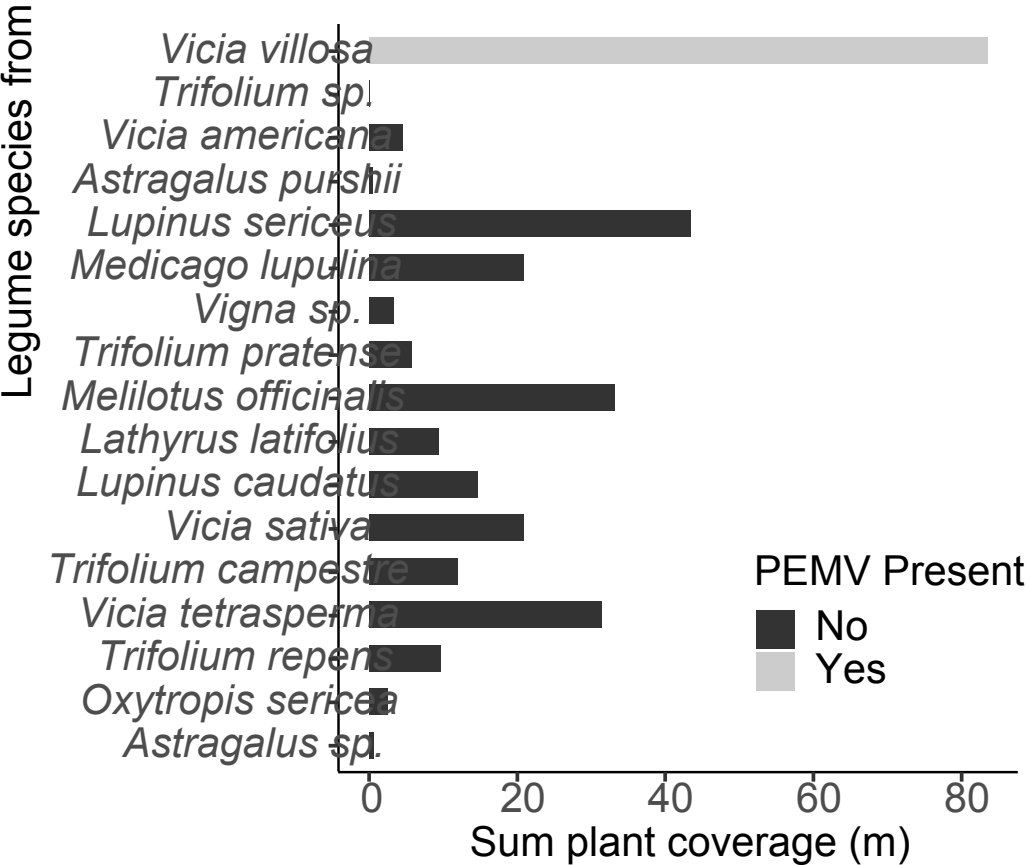
387   Fig 4. Probability predictions from GLMM (binomial fit) for pea aphid presence or absence in

388   transects fitted to the abundance of non-crop host hairy vetch. The line indicates estimates means

389   from GLMM, and the shaded area indicates the standard error of those model predictions. As

390   hairy vetch coverage increased, aphids were more likely to be present in plant communities.

391   Fig. 1

392

393   Fig. 2

395   Fig. 3

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397   Fig. 4

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