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The Plant Vigor Hypothesis applies to a holoparasitic plant on a drought-stressed host

Bethany A. Evans and Victoria Borowicz

4120/School of Biological Sciences, Illinois State University, Normal, IL 61790-4120
USA

Bethany Evans: baevans@ilstu.edu

Victoria Borowicz: vaborow@ilstu.edu

Author for correspondence: Bethany Evans

Bethany Evans
School of Biological Sciences
Illinois State University
Campus Box 4120
Normal, IL 61790-4120 USA
Telephone: 309-438-5587
FAX: 309-438-3722
baevans@ilstu.edu

21 Abstract

22 Parasitic plants extract resources from host vascular tissues but their responses to
23 environmental fluctuation experienced by the host are poorly studied. Three frequently-
24 cited hypotheses for effects of environmental stress on plant resistance to herbivores
25 predict decreased, increased, or fluctuation in herbivore performance in response to
26 drought stress. We tested which hypothesis best accounts for how drought stress applied
27 to a perennial herb affects growth of the holoparasite, *Cuscuta gronovii* (common
28 dodder), an obligate shoot parasite. *Verbesina alternifolia* (wingstem) supporting single,
29 young *C. gronovii* were exposed to continuous, pulsed, or no water stress for 32 d and
30 then dry mass of each parasite was determined. Consistent with the Plant Vigor
31 Hypothesis, *C. gronovii* grew significantly better on well-watered hosts. Continuous and
32 pulsed drought stress of the host resulted in similar growth reduction relative to no
33 drought stress. In addition to reducing absolute growth of the holoparasite, continuous
34 and pulsed drought stress reduced the growth of the holoparasite relative to host growth.
35 Although functionally similar to insect phloem feeders, growth of holoparasites such as
36 *C. gronovii* is constrained by source-sink relations. Our results suggest drought stress
37 experienced by a host weakens source strength and reduces uptake by the holoparasite
38 acting as a sink.

39 Keywords: *Cuscuta gronovii*, drought, host resistance, phloem feeders, *Verbesina*
40 *alternifolia*, parasitic plant

41

42   **Introduction**

43   Approximately 1% of flowering plant species in 18 families are considered to be
44   parasitic (Nickrent 2002; Westwood et al. 2010). This designation is based on formation
45   of a haustorium, an organ bridging host and parasite phloem or xylem (Kujit 1969).
46   Through these structures parasites extract a variety of resources from their hosts,
47   including photosynthates, solutes, and metabolites (Watling and Press 2001; Smith et al.
48   2013). Some parasitic plants, termed holoparasites, are functionally non-photosynthetic.
49   Because these species are fully dependent on hosts for resources transported in the host's
50   xylem and phloem streams, they may be subject to fluctuations in resource availability
51   following water stress experienced by the host.

52   Parasitic plants are important constituents of many terrestrial ecosystems and
53   economically important pests (Parker 2012). Nonetheless, the ecology of parasitic plant-
54   host responses to drought is poorly known. By contrast, drought-mediated interactions
55   between herbivores and host plants have been examined extensively (Huberty and Denno
56   2004, Joern and Mole 2005, Mody et al. 2009, Gutbrodt et al. 2011). Similarities in
57   feeding mode of holoparasitic plants and herbivorous insects (Pennings and Callaway
58   2002; Pennings and Simpson 2008) and hormone signaling in parasitized hosts (Runyon
59   et al. 2010) suggest that hypotheses for effects of plant drought stress on herbivore
60   performance may predict responses of holoparasitic plants.

61   Two long-standing hypotheses postulated to explain patterns of herbivore
62   performance predict opposite effects of environmental stress experienced by the host
63   plant. The **Plant Stress Hypothesis** assumes that stress increases availability of nutrients

64 or decreases secondary metabolites, resulting in greater herbivore preference for or
65 performance on stressed plants (White 1969). The **Plant Vigor Hypothesis** predicts
66 greater herbivore abundance on rapidly-growing, vigorous plants or plant modules for a
67 variety of reasons, including greater concentrations or accessibility of quality nutrients
68 (Price 1991). A third hypothesis, the **Pulsed-stress Hypothesis**, predicts the best
69 performance by phloem, mesophyll, and xylem feeders (sap feeders) on plants
70 experiencing intermittent drought stress because drought induces increases in plant
71 nitrogen compounds that become available to sap feeders when turgor is regained
72 (Huberty and Denno 2004).

73 Here we test the three hypotheses (above) for effects of host plant stress on
74 holoparasite-host interactions. Because their haustoria bridge the parasite and host
75 vascular tissues, holoparasites may be postulated to feed in a manner similar to phloem
76 and xylem feeding herbivores (Marquardt and Pennings 2010; Pennings and Callaway
77 2002; Pennings and Simpson 2008). We relate holoparasites to phloem-feeding
78 herbivores because feeding guild is one of the best predictors of insect response to plant
79 stress (Huberty and Denno 2004; Koricheva et al. 1998) and holoparasites acquire
80 resources primarily from host phloem (Jeschke et al. 1994).

81 We conducted a greenhouse study of the effects of drought stress of the perennial
82 plant *Verbesina alternifolia* (L.) Britton ex Kearney (wingstem) on resistance and
83 tolerance to parasitism by the holoparasite *Cuscuta gronovii* Willd. Ex Schultes (common
84 dodder). The impact of drought stress on host response to parasitism (tolerance) has been
85 published elsewhere (Evans and Borowicz 2013). Here we focus on effects on

86 holoparasite growth as a measure of quantitative resistance to determine which of the
87 three hypotheses best predicts behavior of this holoparasite-host system.

88 Through transport of the small seeds, *Cuscuta* spp. have spread to many parts of the
89 world and are economically important weeds for many crops, including cranberry,
90 clovers, alfalfa, and soybean (Parker 2012). *Cuscuta gronovii* is the most common and
91 abundant species of *Cuscuta* in North America (Sandler 2001). Stems of this annual
92 twine around a host and connect to its vascular tissue via searching hyphae that
93 differentiate into either xylem or phloem elements (Birschwilks et al. 2006). Both
94 *Verbesina alternifolia* (Asteraceae) and *C. gronovii* (Cuscutaceae) grow in thickets,
95 woods, and bottomlands throughout the Midwestern and Eastern United States (Gleason
96 and Cronquist 1991) in areas subject to prolonged or repeated episodes of drought.

98 **Materials and methods**

99 Methods were provided previously (Evans and Borowicz 2013) and details pertinent
100 to performance of *C. gronovii* are summarized here. *Cuscuta gronovii* and *Verbesina*
101 *alternifolia* are both native plants of central Illinois and were found to be in a host-
102 parasite relationship naturally. Seeds of both species collected in Lexington, McLean
103 County, Illinois, USA in October 2010 were cold stratified for 278 d (*V. alternifolia*) or
104 188 d (*C. gronovii*) in plastic bags with damp Perlite™ in a 3°C refrigerator prior to
105 germination. On day 0 (22 d after cold stratification ended) *V. alternifolia* seedlings were
106 transplanted individually into 1.7 L pots containing 1 : 1 MetroMix™ 510 : Perlite™ on
107 greenhouse benches with 14 h of supplemental light. On days 11 and 22 each *V.*

108 *alternifolia* was fertilized with 1 g (12-4-8 N-P-K) of a slow-release granular fertilizer.

109 No pests were observed during the course of the experiment.

110 *C. gronovii* seeds were placed on top of a mixture of soil, sand, and Perlite^{TM} to
111 germinate. On day 12, *C. gronovii* seedlings (3-6 cm long) were placed singly in small, 1
112 dram glass shell vials filled with water and haphazardly assigned to 90 *V. alternifolia*.
113 Vials were placed within 2 cm of the main stem of the host. The seedling was considered
114 to be attached when it completed one tight 360° loop around the host stem and this date
115 was recorded. Bamboo skewer sticks were placed in each pot. Velcro^{TM} strips were used
116 if necessary to secure aggressively growing parasites to the bamboo stick in order to
117 prevent spread to other pots. Therefore, the parasite could only attach to the assigned
118 host. *C. gronovii* made multiple attachments on the host; however the number of
119 attachments was not recorded. Because *V. alternifolia* seeds were collected from the field
120 we anticipated some variation in growth rates due to genotypic differences and conditions
121 experienced by the mother. On day 13 we recorded the length of the longest leaf on each
122 host as a measure of pre-treatment host size.

123 Thirty *V. alternifolia* were randomly assigned to each of three treatments (control,
124 persistently drought stressed, or pulsed drought stressed). On day 25, each pot was
125 watered to excess with 500 ml of water and weighed 30 minutes later to determine initial
126 saturation mass (ISM), a benchmark for all treatments. Control plants were maintained at
127 >85% of ISM. Continuously stressed treatment pots were watered to 45% of ISM after
128 the pot was < 40% of ISM. Pulse-stressed pots received no water until any of 10 sentinel
129 pots declined to 35% ISM, then watered to 100% ISM. Pulse-stressed pots were brought

130 to ISM twice and the experiment was terminated on d 57 when these pots needed a third
 131 pulse of water. Pulsed and continuous drought treatments received similar amounts of
 132 water over the course of the experiment. *Cuscuta gronovii* were removed from host
 133 shoots and dried at 60° C to constant weight. Shoots and roots of *V. alternifolia* were also
 134 harvested, dried, and weighed.

135 Eleven *C. gronovii* failed to attach to the host at least 4 d before drought stress began
 136 and were excluded prior to analysis, ensuring that all parasites were well-established at
 137 the onset of drought stress. Twenty-six controls, 28 pulse-stressed, and 25 continuously-
 138 stressed pots were included in the analyses ($n=79$). Data were transformed to meet the
 139 assumptions of normality and homoscedasticity. All statistical analyses were performed
 140 using SAS 9.2 © 2008.

141 Dry mass of *C. gronovii* was analyzed by analysis of covariance with length of the
 142 longest host leaf as covariate to determine the effects of host water stress on resistance to
 143 parasitism. To determine if the parasite was limited by the amount of the host plant
 144 available, parasite mass g^{-1} of total host mass (shoot and root mass combined) was
 145 analyzed with ANCOVA using duration of attachment to the host as the covariate. When
 146 shade treatment was significant, differences among means were analyzed using
 147 orthogonal comparisons (Sokal and Rohlf 2012).

148 Results

149 Over 45% of the *C. gronovii* attached within one day and 90% within three days of
 150 placement. Drought stress applied to hosts significantly affected the dry mass of *C.*
 151 *gronovii* ($F_{2,75} = 61.73, P<0.0001$). Mean mass of *C. gronovii* on well-watered hosts was

152 >2x that of those on drought-stressed hosts ($F_{1,75} = 123.28$, $P < 0.0001$; Fig. 1A).
153 However, holoparasite growth did not differ between pulsed- and continuously-stressed
154 hosts ($F_{1,75} = 0.68$, $P = 0.4116$). *Cuscuta gronovii* mass increased significantly with the
155 length of the longest host leaf prior to the start of treatments ($F_{1,75} = 4.06$, $P = 0.0474$).

156 Analysis of parasite mass g^{-1} of host indicated that parasite growth was not strictly
157 linked to the amount of host available. Water treatment significantly affected the
158 parasite:host ratio ($F_{2,75} = 3.9$, $P = 0.01$) and *C. gronovii* on well-watered hosts produced
159 more than 25% more dry mass per gram of dry host mass compared to growth on
160 drought-stressed hosts ($F_{1,75} = 7.78$, $P = 0.0067$). Growth of *C. gronovii* per gram of host
161 did not differ between continuously-stressed and pulse-stressed hosts ($F_{1,75} = 0.04$, $P =$
162 0.8458 ; Fig. 1B). Although most *C. gronovii* attached to hosts within 3 days, the duration
163 of attachment ranged from 37 days to 44 days and longer duration of attachment resulted
164 in greater final mass ($F_{1,75} = 6.98$, $P = 0.0100$).

165

166 Discussion

167 Well-watered *V. alternifolia* grew most rapidly (Evans and Borowicz 2013) and
168 supported the largest *C. gronovii*, consistent with the **Plant Vigor Hypothesis**. Interim
169 measurements were not taken and it is possible that pulse-stressed hosts supported more
170 rapid *C. gronovii* growth during intervals of relief from drought. Nonetheless,
171 holoparasite growth over the course of three bouts of intermittent drought stress was
172 similar to growth on continuously-stressed plants, refuting the **Pulse-stress Hypothesis**.

Often portrayed as mutually exclusive, the Plant Vigor and the Plant Stress hypotheses may each usefully describe patterns of herbivore performance if type of tissue consumed is considered (White 2009). Increased performance of phytophages accessing nutrients translocated from mature tissue (“senescence feeders”) is likely to be predicted by the Plant Stress Hypothesis and increased performance of phytophages obtaining nutrients translocated into new growth (“flush feeders”) is likely to be predicted by the Plant Vigor Hypothesis (White 2009). Unlike individual insects, one *Cuscuta* plant maintains multiple haustoria of varying ages on one or more hosts. Due to prolonged attachment and extensive growth, *Cuscuta* and other holoparasites may feed simultaneously as flush-feeders from recent attachments and early in the season when hosts are growing, and as senescence-feeders from older haustoria and later in the season as hosts reallocate metabolites. This hypothesis would be readily tested with *Cuscuta* and suggests avenues for future research. Regardless, in the present experiment, *C. gronovii* clearly performed better on more vigorous, unstressed hosts.

Although holoparasites and aphids feed in analogous ways from the same plant part, the analogy may break down for mechanism of resource acquisition. Using fine stylets, aphids pierce phloem and feed passively due to high turgor pressure within the sieve elements (Guerrieri and Digilio 2008). Transfer of proteins (Haupt et al. 2001), fluorescent dyes (Birschwilks et al. 2006), viruses (Hosford, 1967), and mRNA (Roney et al. 2007) from host to other species of *Cuscuta* strongly suggests symplasmic continuity. Both *C. gronovii* and aphids may have direct contact with host cell contents; however movement to *Cuscuta* occurs because the holoparasite creates a very efficient nutrient sink (Wolswinkel 1984; Vaughn 2006; Smith et al. 2013). Unlike aphids, which are

196 much smaller than their hosts, *C. gronovii* mass can exceed that of its host (Fig. 1b). By
197 creating a strong sink, the holoparasite deprives host roots of carbon, leading to increased
198 host photosynthesis and flow of resources to the holoparasite (Jeschke et al. 1994;
199 Jeschke and Hilpert 1997). Drought-stressed plants close stomata to reduce transpiration
200 and photosynthesis declines (Xu et al. 2010). This reduces uploading and translocation
201 of resources in the phloem stream, decreasing access by the holoparasite. Resistance to
202 parasitism, as measured by holoparasite growth, is consequently greater when hosts are
203 drought stressed.

204 Many climate change models predict increased variability in precipitation and
205 regional droughts (Dore 2005; IPCC 2007). While the impact of drought on plant-
206 herbivore systems has received considerable attention (e.g., Mody et al. 2009; Johnson et
207 al. 2011; Grinnan et al. 2013), less is known about drought effects on parasitic plants as
208 consumers. Similar to insects, holoparasites can be potent pests (Dawson et al. 1994;
209 Sandler 2001; Parker 2010) and have also been considered as agents of biocontrol (Shen
210 et al., 2005; Yu et al. 2009, 2011). Studies that examine the impact of the abiotic
211 environment on holoparasite-host interactions provide context for better understanding
212 the role of holoparasites in natural communities and also as pests and biocontrol agents.
213 Our study indicates that whether continuous or episodic, drought will reduce performance
214 of holoparasites on stricken hosts and the impact is greater than would be accounted for
215 through reduced host growth.

216

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219   discussion, and S.A. Juliano for insightful comments and statistical guidance. Special
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221   this research.

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229   **Data accessibility**

230   Data will be deposited at ISU ReD: Research and eData at
231   <http://ir.library.illinoisstate.edu>

232 **References**

233

234 Birschwilks, M., Haupt, S., Hofius, D., and Neumann, S. 2006. Transfer of phloem-
235 mobile substances from the host plants to the holoparasite *Cuscuta* sp. J. Exp. Bot. **57**:
236 911–921. doi:10.1093/jxb/erj076.

237 Dawson, J.H., Musselman, L.J., Wolswinkel, P., and Dörr, I. 1994. Biology and control
238 of *Cuscuta*. Rev. Weed Sci. **6**: 265-317.

239 Dore, M.H.I. 2005. Climate change and changes in global precipitation patterns: what do
240 we know? Environ. International **31**: 1167-1181. doi:10.1016/j.envint.2005.03.004.

241 Evans, B., and Borowicz, V. 2013. *Verbesina alternifolia* tolerance to the holoparasite
242 *Cuscuta gronovii* and the impact of drought. Plants **2**: 635-649.
243 doi:10.3390/plants2040635.

244 Gleason, H.A., and Cronquist, A. 1991. Manual of vascular plants of Northeastern United
245 States and adjacent Canada. 2d ed. New York Botanical Garden, New York.

246 Grinnan, R., Carter, T.E. Jr, and Johnson, M.T.J. 2013. The effects of drought and
247 herbivory on plant-herbivore interactions across 16 soybean genotypes in a field
248 experiment. Ecol. Entomol. **38**: 290-302. doi:10.1111/een.12017.

249 Guerrieri, E., and Digilio, M.C. 2008. Aphid-plant interactions: a review. J. Plant
250 Interact. **3**:223–232. doi:10.1080/17429140802567173.

251 Gutbrodt, B., Mody, K. and Dorn, S. 2011. Drought changes plant chemistry and causes
252 contrasting responses in lepidopteran herbivores. Oikos **000**: 001–009.
253 doi:10.1111/j.1600-0706.2011.19558.x.

- 254 Haupt, S., Oparka, K.J., Sauer, N., and Neumann, S. 2001. Macromolecular trafficking
255 between *Nicotiana tabacum* and the holoparasite *Cuscuta reflexa*. J. Exp. Bot. **52**:
256 173-177. doi:10.1093/jexbot/52.354.173.
- 257 Hosford, R.M.J. 1967. Transmission of plant viruses by dodder. Bot Rev **42**: 387–406.
258 doi:[10.1104/pp.106.088369](https://doi.org/10.1104/pp.106.088369).
- 259 Huberty A F, and Denno R F. 2004. Plant water stress and its consequences for
260 herbivorous insects: a new synthesis. Ecology **85**: 1383–1398. doi:10.1890/03-0352.
- 261 IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working
262 Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate
263 Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt,
264 M.Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United
265 Kingdom and New York, NY, USA.
- 266 Jeschke, W.D., and Hilpert, A. 1997. Sink-stimulated photosynthesis and sink-dependent
267 increase in nitrate uptake: nitrogen and carbon relations of the parasitic association
268 *Cuscuta reflexa*-*Ricinus communis*. Plant Cell Environ. **20**: 47-56. doi:10.1046/j.1365-
269 3040.1997.d01-2.x.
- 270 Jeschke, W.D., Rath, N., Baumel, P., Czygan, F.C., and Proksch, P. 1994. Modeling the
271 flow and partitioning of carbon and nitrogen in the holoparasite *Cuscuta reflexa* Roxb
272 and its host *Lupinus albus* L. 1. Methods for estimating net flows. J. Exp. Bot. **45**:
273 791–800. doi:10.1093/jxb/45.6.801.
- 274 Joern, A. and Mole, S. 2005. The plant stress hypothesis and variable responses by blue
275 grama grass (*Bouteloua gracilis*) to water, mineral nitrogen, and insect herbivory. J.
276 Chem. Ecol. **31**: 2069–2090. doi:10.1007/s10886-005-6078-3.

- 277 Johnson, S.N., Staley, J.T., McLeod, F.A.L., and Hartley, S.E. 2011. Plant-mediated
278 effect of soil invertebrates and summer drought on above-ground multitrophic
279 interactions. *J. Ecol.* **99**: 57-65. doi:10.1111/j.1365-2745.2010.01748.x.
- 280 Koricheva, J., Larsson, S., and Haukioja, E. 1998. Insect performance on experimentally
281 stressed woody plants: a meta-analysis. *Annu. Rev. Entomol.* **43**: 195–216.
282 doi:10.1146/annurev.ento.43.1.195.
- 283 Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press,
284 Berkeley, California.
- 285 Marquardt, E.S., and Pennings, S.C. 2010. Constraints on host use by a parasitic plant.
286 *Oecologia* **164**: 177–184. doi:10.1007/s00442-010-1664-7.
- 287 Mody, K., Eichenberger, D., and Dorn, S. 2009. Stress magnitude matters: different
288 intensities of pulsed wagner stress produce non-monotonic resistance responses of host
289 plants to insect herbivores. *Ecol. Entomol.* **34**: 133-134. doi:10.1111/j.1365-
290 2311.2008.01053.x.
- 291 Nickrent, D.L. 2002. Parasitic Plants of the World. *In* Parasitic Plants of the Iberian
292 Peninsula and Balearic Islands. *Edited by* J.A. López-Sáez, P. Catalán, and L. Sáez.
293 Mundi-Presna Libros, S.A., Madrid. pp. 7-27.
- 294 Parker, C. 2012. Parasitic Weeds: A World Challenge. *Weed Sci.* **60**: 269–276.
295 doi:10.1614/WS-D-11-00068.1.
- 296 Pennings, S.C., and Callaway, R.M. 2002. Parasitic plants: parallels and contrasts with
297 herbivores. *Oecologia* **131**: 479–489. doi:10.1007/s00442-002-0923-7.
- 298 Pennings, S.C., and Simpson, J.C. 2008. Like herbivores, parasitic plants are limited by
299 host nitrogen content. *Plant Ecol.* **196**: 245-250. doi:10.1007/s11258-007-9348-z.

- 300 Price, P.W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* **62**: 244–251.
- 301 Roney, J.K., Khatibi, P.A., and Westwood, J.H. 2007. Cross-species translocation of
302 mRNA from host plants into the parasitic plant dodder. *Plant Physiol.* **143**: 1037-
303 1043. doi:10.1104/pp.106.088369.
- 304 Runyon, J.B., Mescher, M.C., Felton, G.W., and De Moraes, C.M. 2010. Parasitism by
305 *Cuscuta pentagona* sequentially induces JA and SA defence pathways in tomato.
306 *Plant Cell Environ.* **33**: 290-303. doi:10.1111/j.1365-3040.2009.02082.x.
- 307 Sandler, H.A. 2001. Dodder - *Cuscuta gronovii* Willd. Cranberry Experiment Station,
308 University of Massachusetts, Wareham, MA.
- 309 Shen, H., Ye, W., Hong, L., Cao, H., and Wang, Z. 2005. Influence of the obligate
310 parasite *Cuscuta campestris* on growth and biomass allocation of its host *Mikania*
311 *micrantha*. *J. Exp. Bot.* **56**: 1277-1284. doi:10.1093/jxb/eri128.
- 312 Smith, J.D., Mescher, M.C., and De Moraes, C.M. 2013. Implications of bioactive solute
313 transfer from hosts to parasitic plants. *Curr. Opin. Plant Biol.* **16**: 464-472.
314 doi:10.1016/j.pbi.2013.06.016.
- 315 Sokal, R.R., and Rohlf, F.J. 2012. Biometry: The principles and practice of statistics in
316 biological research. 4th ed., W.H. Freeman and Co., New York.
- 317 Vaughn, K.C. 2006. Conversion of the searching hyphae of dodder into xylem and phloem
318 hyphae: a cytochemical and immunocytochemical investigation. *Int. J. Plant Sci.* **167**:
319 1099–1114. doi:10.1086/507872.
- 320 Watling, J.R. and Press, M.C. 2001. Impacts of infection by parasitic angiosperms on
321 host photosynthesis. *Plant Biol.* **3**: 244–250. doi:10.1055/s-2001-15195.

- 322 Westwood, J.H., Yoder, J.I., Timko, M.P., dePamphilis, C.W. 2010. The evolution of
323 parasitism in plants. *Trends in Plant Science* **15**: 227–235.
324 doi:10.1016/j.tplants.2010.01.004.
- 325 White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with
326 outbreaks of psyllids in Australia. *Ecology* **50**: 905–909. doi:10.2307/1933707.
- 327 White, T.C.R. 2009. Plant vigour versus plant stress: a false dichotomy. *Oikos* **118**: 807-
328 808. doi:10.1111/j.1600-0706.2009.17495.x.
- 329 Wolswinkel, P. 1984. Phloem unloading and ‘sink strength’: the parallel between the
330 site of attachment of *Cuscuta* and developing legume seeds. *Plant Growth Regulation*
331 **2**: 309-317. doi:10.1007/BF00027290.
- 332 Xu, Z., Zhou, G., and Shimizu, H. 2010. Plant responses to drought and rewatering. *Plant*
333 *Signal. Behav.* **5**: 649-654. doi:10.4161/psb.5.6.11398.
- 334 Yu, H., Liu, J., He, W.M., Miao, S.L., and Dong, M. 2009. Restraints on *Mikania*
335 *micrantha* by *Cuscuta campestris* facilitates restoration of the disturbed ecosystem.
336 *Biodiversity* **10**: 72-78. doi:10.1080/14888386.2009.9712847.
- 337 Yu, H., Liu, J., He, W.M., Miao, S.L., and Dong, M. 2011. *Cuscuta australis* restrains
338 three exotic invasive plants and benefits native species. *Biol. Invasions* **13**: 747-756.
339 doi:[10.1093/aobpla/plv031](https://doi.org/10.1093/aobpla/plv031).

340 Figure captions.

341 Fig. 1. Least squares mean ($\pm$ s.e.) of *C. gronovii* (a) dry mass, and (b) dry mass g⁻¹ dry host
342 mass when the host *V. alternifolia* was well watered, pulse-stressed, or continuously drought
343 stressed. *** = $P < 0.0001$. ** = $P < 0.01$.

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Draft