Competitive interactions between a nonmycorrhizal invasive plant, *Alliaria petiolata*, and a suite of mycorrhizal grassland, old field, and forest species

Gary T Poon, Hafiz Maherali

The widespread invasion of the nonmycorrhizal biennial plant, *Alliaria petiolata* in North America is hypothesized to be facilitated by the production of novel biochemical weapons that suppress the growth of mycorrhizal fungi. As a result, *A. petiolata* is expected to be a strong competitor against plant species that rely on mycorrhizal fungi for nutrient uptake services. If *A. petiolata* is also a strong competitor for soil resources, it should deplete nutrients to levels lower than can be tolerated by weaker competitors. Because the negative effect of losing the fungal symbiont for mycorrhizal plants is greatest when nutrients are low, the ability of *A. petiolata* to simultaneously suppress fungi and efficiently take up soil nutrients should further strengthen its competitive ability against mycorrhizal plants. To test this hypothesis, we grew 27 mycorrhizal tree, forb and grass species that are representative of invaded habitats in the absence or presence of competition with *A. petiolata* in soils that had previously been experimentally planted with the invader or left as a control. A history of *A. petiolata* in soil reduced plant available forms of nitrogen by >50% and phosphorus by 17% relative to control soil. Average mycorrhizal colonization of competitor species was reduced by >50% in *A. petiolata* history versus control soil. Contrary to expectations, competition between *A. petiolata* and other species was stronger in control than history soil. The invader suppressed the biomass of 70% of competitor species in control soil but only 26% of species in history soil. In addition, *A. petiolata* biomass was reduced by 56% in history versus control soil, whereas the average biomass of competitor species was reduced by 15%. Thus, our results suggest that the negative effect of nutrient depletion on *A. petiolata* was stronger than the negative effect of suppressing mycorrhizal colonization on competitor species. These findings indicate that the inhibitory potential of *A. petiolata* on competitor species via mycorrhizal suppression is not enhanced under nutrient limitation.

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5 **suite of mycorrhizal grassland, old field, and forest species**

9 Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1

12 Gary T. Poon and Hafiz Maherali[1]

14 [1]corresponding author: Hafiz Maherali, Department of Integrative Biology, University of

15 Guelph, 50 Stone Road East, Guelph, ON, CANADA; 519-824-4120 ext. 52767;

16 maherali@uoguelph.ca

Abstract

24   The widespread invasion of the nonmycorrhizal biennial plant, *Alliaria petiolata* in North

25   America is hypothesized to be facilitated by the production of novel biochemical weapons that

26   suppress the growth of mycorrhizal fungi. As a result, *A. petiolata* is expected to be a strong

27   competitor against plant species that rely on mycorrhizal fungi for nutrient uptake services. If *A.*

28   *petiolata* is also a strong competitor for soil resources, it should deplete nutrients to levels lower

29   than can be tolerated by weaker competitors. Because the negative effect of losing the fungal

30   symbiont for mycorrhizal plants is greatest when nutrients are low, the ability of *A. petiolata* to

31   simultaneously suppress fungi and efficiently take up soil nutrients should further strengthen its

32   competitive ability against mycorrhizal plants. To test this hypothesis, we grew 27 mycorrhizal

33   tree, forb and grass species that are representative of invaded habitats in the absence or presence

34   of competition with *A. petiolata* in soils that had previously been experimentally planted with the

35   invader or left as a control. A history of *A. petiolata* in soil reduced plant available forms of

36   nitrogen by >50% and phosphorus by 17% relative to control soil. Average mycorrhizal

37   colonization of competitor species was reduced by >50% in *A. petiolata* history versus control

38   soil. Contrary to expectations, competition between *A. petiolata* and other species was stronger

39   in control than history soil. The invader suppressed the biomass of 70% of competitor species in

40   control soil but only 26% of species in history soil. In addition, *A. petiolata* biomass was reduced

41   by 56% in history versus control soil, whereas the average biomass of competitor species was

42   reduced by 15%. Thus, our results suggest that the negative effect of nutrient depletion on *A.*

43   *petiolata* was stronger than the negative effect of suppressing mycorrhizal colonization on

44   competitor species. These findings indicate that the inhibitory potential of *A. petiolata* on

45   competitor species via mycorrhizal suppression is not enhanced under nutrient limitation.

Introduction

47 Invasions by exotic species are common and can negatively influence the structure and function

48 of invaded communities and ecosystems (Pimental et al., 2000). Designing effective control and

49 eradication programs to limit the spread of an invasive species, however, requires identifying the

50 specific mechanism that facilitated invasion (Mack et al., 2000). Numerous mechanisms have

51 been identified to explain successful invasions (Catford et al., 2009; Gurevitch et al., 2011). For

52 example, successful invaders may have high propagule production (Colautti et al., 2006), possess

53 or evolve superior competitive ability for limiting resources (Blossey & Notzold, 1995), be

54 released from specialist antagonists in their native range (Callaway et al., 2004), possess the

55 ability to acclimate to a wide variety of conditions (Parker et al., 2003), or secrete novel

56 biochemical compounds that reduce the performance and survival of native inhabitants

57 (Callaway & Ridenour, 2004).

58   Recent reviews suggest that successful invasions rarely occur because of a single

59 mechanism (Catford et al., 2009; Gurevitch et al., 2011). At least three explanations for weak

60 effects of any one mechanism have been proposed (Gurevitch et al., 2011). First, the efficacy of

61 a particular mechanism may depend on ecological context, where differences in resource

62 availability and the functional attributes of resident species can either facilitate or increase

63 resistance to invasion (Funk et al., 2008). Second, the importance of a particular mechanism

64 could differ between phases of an invasion (Dietz & Edwards, 2006). For example, allelopathy

65 may effectively suppress resident species in the initial phases of invasion (Callaway & Ridenour,

66 2004), but its effects can diminish as resident species acclimate or evolve resistance to the novel

67 biochemicals (Lankau et al., 2009; Lankau, 2011). Third, multiple mechanisms could act

68 synergistically, as observed in situations where invasion is facilitated by both competitive

69 suppression of resident species and reduced palatability to herbivores (Lau & Schultheis, 2015).

70 Simultaneous empirical assessments of multiple causes of invasion, however, are infrequent

71 (Zheng et al., 2015).

72   The widespread invasion of *Alliaria petiolata* ((M. Bieb.) Cavara & Grandem,

73   Brassicaceae), a biennial species native to Europe that was introduced to North America in the

74   late 19th century (Cavers et al., 1979), has been attributed to several factors (Rodgers et al.,

75   2008a). Of these mechanisms, the ability of *A. petiolata* to produce allelopathic phytochemicals

76   has received considerable attention. *A. petiolata* phytochemicals are present in leaf litter and also

77   released as root exudates (Cipollini et al., 2005; Rodgers et al., 2008a), but have limited direct

78   negative effects on neighboring plant species (McCarthy & Hanson, 1998; Roberts & Anderson,

79   2001; Prati & Bossdorf, 2004; Cipollini et al., 2008). Instead, *A. petiolata* phytochemicals tend to

80   suppress the growth of mycorrhizal fungi (Roberts & Anderson, 2001; Stinson et al., 2006;

81   Callaway et al., 2008; Rodgers et al., 2008a; Wolfe et al., 2008; Cantor et al., 2011), though the

82   effect is variable (Burke, 2008; Lankau et al., 2009; Lankau, 2011). Because *A. petiolata* is non-

83   mycorrhizal, whereas most plant species rely on mycorrhiza for nutrient uptake services (Wang

84   & Qiu, 2006; Brundrett, 2009), the suppression of mycorrhizal fungi is expected to advantage *A.*

85   *petiolata* relative to other species during establishment (Stinson et al., 2006; Callaway et al.,

86   2008; Hale & Kalisz, 2012), though this effect can diminish over time (Lankau et al., 2009;

87   Lankau, 2011).

88   The successful establishment and persistence of *A. petiolata* may also be influenced by

89   the joint effects of novel biochemical weapons and the ability to acquire soil resources more

90   effectively than potential competitors (Blossey & Notzold, 1995). Resource competition theory

91   predicts that the strong competitors deplete limiting resources to levels lower than weaker

92   competitors (Tilman, 1988; Tilman & Wedin, 1991; Bever et al., 2010). If *A. petiolata* is a strong

93   resource competitor, it should deplete soil nutrients below tolerable limits for other species,

94   suppressing other species more than itself. The ability to efficiently take up nutrients as well as

95   survive and reproduce under limited soil nutrients could explain *A. petiolata*'s ability to colonize

96   habitats that vary widely in nutrient availability (Rodgers et al., 2008b) as well its ability to

97   suppress native vegetation (e.g., Stinson et al., 2007; Rodgers et al., 2008a). Moreover, if *A.*

98   *petiolata* can suppress mycorrhizal fungi while simultaneously depleting soil nutrients, this

99 should result in even stronger suppression of mycorrhizal competitors. This is because the

100 negative effect of losing the fungal symbiont is greatest when mycorrhizal plants are grown in

101 low soil nutrients (Hoeksema et al., 2010; Johnson, 2010).

102   Despite the potential for *A. petiolata* to modify the soil environment in a way that

103 enhances its own competitive ability, resident species may still be able to resist invasion. Such

104 resistance could depend on the morphological and physiological traits that influence acquisition

105 of soil nutrients and light, which most often limit plant growth (Grime, 1977; Gaudet & Keddy,

106 1988; Goldberg & Landa, 1991; Wardle et al., 1998; Funk et al., 2008). The potential for

107 depletion of soil nutrients and the suppression of mycorrhizal fungi by *A. petiolata* suggests that

108 resident species which resist competitive suppression should have thin roots that maximize

109 absorptive root surface area for resource uptake (Goldberg, 1996; Casper & Jackson, 1997). In

110 addition, species that successfully resist invasion by *A. petiolata* could also be effective at

111 acquiring light (Stinson & Seidler, 2014), particularly by accelerated height growth, which

112 would allow them to overtop neighbors, and by having high photosynthetic light use efficiency

113 (Gaudet & Keddy, 1988; Goldberg & Landa, 1991; Rosch et al., 1997; Keddy et al., 2002; Wang

114 et al., 2010). The competitive ability of *A. petiolata* against other species has been tested in

115 pairwise competition trials (Meekins & McCarthy, 1999; Rodgers et al., 2008a; Lankau, 2010;

116 Leicht-Young et al., 2012), but whether growth in previously invaded soils enhances its

117 competitive ability against mycorrhizal plant species is not known (Hale & Kalisz, 2012; Smith

118 & Reynolds, 2014).

119   To test the hypothesis that nutrient depletion in the first year of an invasion enhances the

120 competitive ability of *A. petiolata* against resident mycorrhizal plant species in subsequent years,

121 we grew *A. petiolata* with and without multiple competitor species in forest soil that had either

122 been left intact or previously planted with *A. petiolata*. This latter treatment simulates a reduction

123 in soil nutrient availability because *A. petiolata* is expected to take up resources during growth.

124 However, the experiment does not strictly mimic the entire process of invasion in the field

125 because the high decomposability of *A. petiolata* leaves is expected to return nutrients to soil in

126   the longer term (e.g., Rodgers et al., 2008b). The experimental design nonetheless allows us to

127   address whether the competitive ability of *A. petiolata* can be influenced by changes in overall

128   resource availability. Because *A. petiolata* occurs in a wide variety of habitats, including old

129   fields, road sides, forest edges and forest understories (Cavers et al., 1979; Stinson & Seidler,

130   2014; Smith & Reynolds, 2014; Biswas et al., 2015), we quantified competition between *A.*

131   *petiolata* and 27 native and non-native mycorrhizal competitor species that represent these

132   different habitats (e.g., Cavers et al., 1979). We predicted that soil nutrient reduction and the

133   potential for inhibition of mycorrhizal fungi by previous growth of *A. petiolata* in soil ('history

134   soil') inhibits the growth of mycorrhizal plant species. As a result, *A. petiolata* should more

135   strongly suppress the growth of, and resist growth suppression by, competitor species in the

136   history soil treatment than in control soil. We predicted that competitor species with finer roots,

137   greater height extension, and higher photosynthetic efficiency would be more likely to resist

138   competition against *A. petiolata*.

139

140   **Materials and Methods**

141   To examine competitive interactions between resident species and *A. petiolata*, we grew 27

142   target species with and without the presence of *A. petiolata* (Table 1). Competitor species

143   included forest trees, forest understory herbs, old field herbs and grasses that are commonly

144   found in areas typically invaded by *A. petiolata* in southern Ontario (e.g., Biswas et al., 2015).

145   *Alliaria petiolata* seeds were bulk collected from the Wild Goose Woods, a mixed hardwood

146   forest in the University of Guelph Arboretum (43° 32'N, 80° 12'W) in July 2009. *Alliaria*

147   *petiolata* can be found in dense patches along the periphery of the forest throughout this site.

148   Seeds for each competitor species were harvested within the Guelph Arboretum as well as

149   purchased from suppliers [Acorus Restoration, Walsingham, ON; Angelgrove Seed Company,

150   Harbour Grace, NL, Ontario Tree Seed Facility, Angus, ON; Richter's Herbs, Goodwood, ON

151   (Table 1)].

152   To simulate a soil environment that *A. petiolata* is likely to encounter upon invasion, we

153  grew plants in a forest soil without a history of *A. petiolata.* In November 2009, soil was

154  collected to a depth of 30 cm from a mixed deciduous forest dominated by *Acer saccharum* in

155  the Koffler Scientific Reserve (44° 03' N, 79° 29' W, Newmarket, ON). Prior to soil collection,

156  live aboveground vegetation and macro-organic matter (leaves and twigs) were removed. Soil

157  was sieved onsite to remove roots and stones and placed into 30, 35L tubs (60.7 cm long × 40.4

158  cm wide × 22.1 cm deep; Roughneck Storage Box #2214, Newell Rubbermaid Inc, Atlanta, GA).

159  Tubs had holes drilled in the bottom to facilitate drainage. Soils were stored at 4 °C prior to the

160  beginning of experiments. To experimentally create a treatment where the presence of *A.*

161  *petiolata* has modified the soil, we grew *A. petiolata* plants in half of the field collected soil (e.g.,

162  Callaway et al., 2008). The remaining soil was left intact in the tubs. To create the *A. petiolata*

163  soil history treatment, *A. petiolata* seeds were cold stratified at 4°C for 120 days on moist filter

164  paper placed inside 10 cm diameter parafilm sealed petri dishes. In January 2010, 100

165  germinating *A. petiolata* seeds were transplanted into each of 15 randomly selected tubs. After 6

166  weeks, seedlings were thinned to a density of 80 plants/m^2, which approximates the upper end of

167  *A. petiolata* density in field populations (Meekins & McCarthy, 2002). Tubs containing *A.*

168  *petiolata* seedlings and those containing intact control soil were randomly arranged on the

169  greenhouse bench and watered to maintain field capacity. Germinating seedlings from other

170  species were periodically removed from all tubs. *Alliaria petiolata* plants were harvested 5

171  months after germination to simulate the approximate active growing season for first year

172  rosettes of this species in southern Ontario and to allow roots to fully explore the soil in the tubs.

173  At harvest, the aboveground portion of plants was removed and discarded, and soil was sieved to

174  remove roots and homogenized within each soil treatment.

175   To quantify the effect of *A. petiolata* history on soil nutrients, we sampled 500 mL of soil

176  from the post-harvest homogenized soil mixture for each treatment and analyzed it for plant

177  available nutrients, including NO_3^-, NH_4^+, P (Olsen), Mg, and K in mg per unit mass (kg) or

178  volume (L) of soil (University of Guelph Laboratory Services;

179   www.guelphlabservices.com/AFL/plants.aspx). Soil that had been left without *A. petiolata*

180   contained 160 mg/kg NO_3^-,18.3 mg/kg NH_4^+, 23 mg/L P, 77 mg/L Mg, and 52 mg/L K. In soil

181   with *A. petiolata* history, these amounts were reduced to 29.2 mg/kg for NO_3^- (-82% decrease),

182   8.56 mg/kg for NH_4^+ (-53% decrease), 19 mg/L for P (-17% decrease), 53 mg/L for Mg (-31%

183   decrease) and 40 mg/L for K (-23% decrease).

184   To study the effects of soil treatment, interspecific competition and competitive species

185   identity on the growth of either *A. petiolata* or the competitor, we used a three-factor design. To

186   quantify competition, we grew each competitor species in the presence and absence of an *A.*

187   *petiolata* individual in the same pot (e.g., Gaudet & Keddy, 1988; Wang et al., 2010) in both soil

188   treatments. We also grew *A. petiolata* alone as a reference to calculate its response to

189   competition with the other species. Each treatment combination [(27 species + *A. petiolata*) × 2

190   soil treatments × 2 competition treatments] was replicated 6 times for a total of 744 pots. Pots

191   (650 mL volume, 6.4 cm wide × 25 cm deep; D40 R, Stuewe and Sons Inc., Tangent, OR) were

192   filled with either *A. petiolata* history or untreated field soil and were randomly arranged in a

193   checkerboard pattern across 53 trays (57 N25T, Stuewe and Sons, Inc., Tangent, OR) to

194   minimize competition for light between pots. To induce germination, all seeds were cold

195   stratified for 30-120 days based on information provided by seed suppliers. Cold stratification

196   times were staggered to ensure all species germinated at the same time. After stratification, seeds

197   were moved to the University of Guelph Phytotron greenhouse and germinated in a medium of

198   2/3 top soil and 1/3 silica sand and then transplanted into experimental treatments. Because of

199   slow germination in some species, they were planted in two groups separated by two weeks. All

200   plants were grown for the same number of days and were completely randomized across the

201   greenhouse benches. 100 mL of ¼ strength 18-9-18 N:P:K fertilizer (Plant Products,

202   Leamington, ON) was added once to all pots in both soil treatments to promote seedling

203   establishment. Because an equal amount of fertilizer was added to all pots, nutrient differences

204   between the *A. petiolata* history and control soil treatments remained. After 63 days, when

205 herbaceous competitor plants had reached reproductive maturity, the aboveground parts of plants

206 were harvested, separated according to species, dried at 60°C for 48 hours and weighed.

207 To determine if *A. petiolata* soil history suppressed arbuscular mycorrhizal (AM) fungi,

208 we harvested the roots of a subset of competitor species when grown alone in both history and

209 control soil. To quantify root colonization by AM fungi, we selected eight species that

210 represented the range of growth forms in the experiment. Root cell contents were cleared with

211 potassium hydroxide and AM fungi were stained with Chlorazol black E (Brundrett et al., 1984).

212 Samples were mounted on glass slides and viewed under a compound microscope at 250×

213 magnification. To quantify fungal colonization by AM hyphae, arbuscules, and vesicles, we used

214 the gridline intersection method (McGonigle et al., 1990). Colonization was quantified as the

215 presence or absence of well-stained structures at 50 intersections per root sample.

216 To determine whether morphological and physiological traits could explain the ability of

217 competitive species to either resist suppression by, or suppress *A. petiolata*, we measured

218 aboveground traits on all plant species in the absence of competition in both soil treatments. We

219 measured leaf chlorophyll concentration and photosynthetic efficiency of up to 6 individuals

220 from each species in each soil treatment at 5 and 9 weeks growth. Height at 5 weeks on these

221 individuals was recorded as the vertical distance from the soil surface to the tip of the tallest leaf.

222 We measured chlorophyll concentration on the three youngest fully expanded leaves per plant

223 using a portable chlorophyll meter (SPAD 502, Minolta, Inc., Ramsey, NJ), and calculated an

224 average value per plant. We measured photosynthetic efficiency as instantaneous fluorescence

225 yield under saturating light conditions (1500 μmol m^{-2} s^{-1}), a measure of the light use efficiency

226 of photosystem II (Maxwell & Johnson, 2000). The three youngest fully expanded leaves per

227 plant were measured using a light-adapted fluorometer (PAM-2500, Heinz Walz APbH,

228 Effeltrich, Germany) and an average value per plant was calculated.

229 To determine if root traits co-varied with competitive ability, we grew 5 replicates of all

230 plant species in a separate experiment in a sterilized mixture of 2/3 silica sand and 1/3 topsoil for

231 35 days. Root architecture could not be measured in the main experiment because roots could not

232   be effectively separated from the higher organic matter containing field soil, and because roots

233   were becoming pot bound by the time of harvest. The shorter growing period and silica sand-

234   topsoil mixture prevented plant roots from becoming pot bound and facilitated the harvest of

235   intact root systems. Plants were grown individually in 650 mL pots (D40 R, Stuewe and Sons

236   Inc., Tangent, Oregon, USA). At harvest, roots were cleaned and preserved in 50% ethanol. For

237   analysis, roots were stained with 0.05% Toluidine Blue O to improve the visibility of fine roots,

238   spread out in water to minimize overlap and photographed with a high resolution (6400 dpi)

239   scanner (Epson V700, Epson Canada Limited, Markham, ON). Root images were analyzed with

240   WinRhizo software (version 2009a; Regent Instruments 2009, Quebec City, QC) using the

241   automatic pixel classification setting to assess the length and average root diameter of each root

242   system. After scanning, roots were dried at 60°C for 48 hours and weighed. In addition to

243   average root diameter, we also calculated specific root length (SRL), or the ratio of root length to

244   root mass, which is indicative of the amount of surface area available for nutrient absorption

245   (Craine et al., 2001).

246   To assess the magnitude and variation in resistance of competitor species to *A. petiolata*

247   competition and whether the magnitude of resistance is influenced by *A. petiolata* soil history,

248   we analyzed aboveground biomass of competitor species with a three-way analysis of variance

249   (ANOVA) with competition, soil history and competitor species identity and all interactions as

250   factors. Planned orthogonal single degree of freedom (1-df) contrasts were used to determine

251   whether each competitor species biomass differed between competition treatments within each

252   soil history treatment. We also used 1-df contrasts to test whether growth forms (trees, forbs,

253   grasses) differed as a whole between competition treatments in each soil history treatment.

254   To assess the magnitude and variation in the ability of competitor species to influence *A.*

255   *petiolata* aboveground biomass, and whether this species effect was influenced by soil history,

256   we used a two-way ANOVA with competitor species identity, soil history and their interaction as

257   factors. To test whether growth with a competitor species suppressed the biomass of *A. petiolata*

258   in each soil treatment, we used planned orthogonal 1-df contrasts to compare the biomass of *A.*

259   *petiolata* grown alone relative to its growth i) with each competitor, ii) with each growth form in

260   aggregate, and iii) across all competitor species in aggregate. The effect of soil treatment on

261   fungal colonization of roots was determined with a two-way ANOVA with soil and species as

262   factors. The statistical significance of soil treatment on fungal colonization for each species was

263   determined by comparing 95% confidence intervals for overlap. The effect of growth form and

264   soil treatment on plant traits was tested with a two-way ANOVA using species means for each

265   trait as the replicate. Differences among growth forms were determined by comparing the 95%

266   confidence intervals for each growth form for overlap following a significant main effect. All

267   ANOVAs and 1-df contrasts were done with SPSS 22.0 (IBM Corp., Armonk, NY).

268   To quantify variation in the ability of competitor species to either resist suppression by *A.*

269   *petiolata* or suppress *A. petiolata*, we calculated two indices of competition. The ability of a

270   competitor species to resist suppression is defined as competitive response (CR, Wang et al.,

271   2010), and was quantified as ln(biomass under competition/biomass alone). The ability of each

272   competitor species to suppress *A. petiolata* is defined as competitive effect (CE, Gaudet &

273   Keddy, 1988; Wang et al., 2010), and was quantified as −ln(*A. petiolata* biomass under

274   competition/*A. petiolata* biomass alone). When calculated this way, greater values reflect

275   stronger competitive ability.

276   To determine whether morphological and physiological traits of competitor plants were

277   associated with competitive ability, we used phylogenetic generalized least squares (PGLS)

278   multiple regression, with competitive ability (either CR or CE) as the dependent variable and

279   traits as independent variables. Growth form of plants was used as a covariate in the analysis.

280   Because root traits were assessed in a different experiment, multiple regression analyses were

281   run separately for aboveground and belowground traits. To analyze data, we used the time

282   calibrated phylogenetic tree from Davies et al. (2004) in Phylomatic (Webb et al., 2008), pruned

283   to include the competitor species. In PGLS regression, the phylogenetic variance-covariance

284   matrix is incorporated into the calculation of coefficients (β) for either a univariate or multiple

285   regression model (Martins & Hansen, 1997; Pagel, 1999). To calculate the magnitude of

286 phylogenetic effects on the regression, maximum likelihood is used to estimate λ, an index which

287 varies from 0, indicating complete independence between variation in the regression residuals

288 and phylogeny, and 1, indicating complete dependence between residual variation with

289 Brownian model of evolution (Freckleton et al., 2002). When λ = 0, the PGLS regression is

290 identical to ordinary least squares regression. PGLS regression and estimates of λ were done in R

291 version 3.12 (R Core Team, 2015) using the 'pgls' command in the package caper, version 0.5.2

292 (Orme et al., 2013).

293

294 **Results**

295 The average aboveground biomass of competitor species was reduced by the presence of

296 *A. petiolata* compared to when they were grown alone (significant competition main effect,

297 Table 2). However, competition was weaker in soil with a history of *A. petiolata* relative to

298 control soil (significant soil history × competition interaction, Table 2, Fig. 1). The average

299 biomass of competitor species was reduced by 59% in control soil compared to 27% in *A.*

300 *petiolata* history soil. The influence of soil history on competition also varied among species

301 (significant species × soil history × competition interaction, Table 2, Fig.1). For example, the

302 aboveground biomass of 19 species (70%; 13/18 native, 6/9 introduced) was suppressed by

303 competition in control soil whereas only 7 species (26%; 4/18 native, 3/9 introduced) were

304 suppressed by competition in *A. petiolata* history soil. On a growth form basis, trees (-38%, $P =$

305 0.01), forbs (-62%, $P < 0.000001$) and grasses (-56%, $P < 0.000001$) were all suppressed by *A.*

306 *petiolata* in control soil, whereas the biomass of forbs (-32%, $P < 0.000001$) and grasses (-14%,

307 $P = 0.007$), but not trees ($P = 0.228$), was significantly reduced by competition in the *A. petiolata*

308 history soil (Fig.1, insets).

309 The average biomass of *A. petiolata* in competition was not significantly different from

310 its average biomass when grown alone in either soil treatment ($P_{history} = 0.284$, $P_{control} = 0.602$;

311 Fig. 2). *Alliaria petiolata* biomass varied in response to competition with different competitor

312 species (significant species effect, Table 3, Fig. 2). In most cases, these species effects were not

313   consistent between control and history soils (significant species × soil history interaction, Table

314   3). For example, relative to its biomass when alone, *A. petiolata* was significantly smaller in

315   competition with *H. matronalis, B. inermis, E. canadensis, E. riparius,* and *E. virginicus* in

316   control soil but significantly smaller in competition with *Q. macrocarpa, H. matronalis* and *E.*

317   *canadensis* in history soil (Fig. 2). In some cases, *A. petiolata* biomass was higher when grown

318   with a competitor species than when grown alone. This response occurred with *P. strobus* and *T.*

319   *occidentalis* in control soil and *H. perforatum* in history soil. *A. petiolata* biomass response to

320   competition also varied with growth form, and this effect differed between soil treatments (Fig.

321   2, insets). In control soil, *A. petiolata* biomass was 27% higher ($P = 0.041$) when grown with

322   trees than when grown alone, 43% lower ($P = 0.001$) when grown with grasses than when grown

323   alone, and not influenced by forbs ($P = 0.61$). In history soil, *A. petiolata* biomass was not

324   affected by competition with trees ($P = 0.96$) or forbs ($P = 0.38$), but was 62% lower ($P = 0.033$)

325   when grown with grasses than when grown alone.

326   On average, competitor species grown alone in soil with a history of *A. petiolata* were

327   15% smaller than plants grown in control soil ($F_{1,261} = 21.991$, $P = 0.000004$, Fig. 3). Competitor

328   species also differed in their response to *A. petiolata* soil history ($F_{26,261} = 3.042$, $P = 0.000003$),

329   though a majority showed no significant difference between treatments. Significant negative

330   effects of soil history were found for *Q. macrocarpa* (-37%, $P = 0.041$), *H. matronalis* (-29%, *P*

331    $= 0.041$), *R. hirta* (-43%, $P < 0.000001$), *E. riparius* (-20%, $P = 0.048$), and *P. virgatum* (-33%,

332    $P < 0.000001$). The strongest negative response to soil history was observed for *A. petiolata*,

333   whose biomass was 56% lower in soil in which it had been previously planted than in control

334   soil ($P = 0.004$).

335   Plants grown in soils with a history of *A. petiolata* had reduced levels of arbuscular

336   mycorrhizal colonization of roots (Fig. 4). On average, plants in the soil history treatment had

337   57% reduced hyphal colonization ($F_{1,60} = 20.47$, $P = 0.000029$), 53% reduced arbuscular

338   colonization ($F_{1,60} = 4.97$, $P = 0.029$), and 57% reduced vesicular colonization ($F_{1,60} = 4.95$, $P =$

339   0.030) than plants grown in control soils. These effects were strongest in *Q. macrocarpa, F.*

340   *virginiana* and *E. canadensis* for hyphae (Fig. 4a), *H. perforatum* for arbuscles (Fig. 4b) and *F.*

341   *virginiana* for vesicles (Fig 4c). We note that *Q. macrocarpa* is not typically colonized by AM

342   fungi (Table 1), and so the levels of fungal colonization reported for this species may reflect a

343   non-functional symbiosis. The average sizes of the soil history effect on colonization with *Q.*

344   *macrocarpa* removed from the dataset were -53% for hyphae ($F_{1,51} = 14.7$, $P = 0.000353$), -

345   52.5% for arbuscles ($F_{1,51} = 4.63$, $P = 0.036$) and -54.5% for vesicles ($F_{1,51} = 3.38$, $P = 0.072$),

346   Morphological and physiological traits of competitor plants grown alone differed among

347   growth forms, but were not generally affected by growing in soil with a history of *A. petiolata*

348   (Fig. 5). Quantum yield of photosystem II [Y(II)] measured at week 5 was significantly higher in

349   herbs and grasses relative to trees. In week 9, Y(II) was significantly higher in herbs compared to

350   grasses and trees (Fig 5a). The quantum yield of photosystem II did not differ between soil

351   treatments in week 5, but was lower in *A. petiolata* history soil than control soil in week 9.

352   Chlorophyll concentration in week 5 was significantly higher in herbs and grasses than trees, but

353   did not differ among growth forms in week 9, and did not differ between soil history treatments

354   (Fig. 5b). At week 5, grasses were significantly taller than trees and herbs, but height was not

355   influenced by soil history treatment (Fig. 5c). Trees had significantly larger root diameter than

356   either herbs or grasses, which did not differ significantly from each other. Trees also had

357   significantly lower SRL than herbs, whereas grasses had intermediate SRL that did not differ

358   significantly from that of trees or herbs (Fig. 5d & 5e).

359   Though above and belowground functional traits varied among growth forms, these traits

360   were generally not associated with their ability to compete in either soil environment, measured

361   as either the ability to resist suppression from (competitive response, CR) or suppress

362   (competitive effect, CE) *A. petiolata* (Table 4). The only exception to this pattern was the nearly

363   significant ($P = 0.06$) positive relationship between Y(II) @ 5 weeks and competitive response in

364   *A. petiolata* history soil. In addition, even though species varied in their response to soil history,

365   this variation was also not correlated with competitive ability. The ln response ratio of growth in

366   *A. petiolata* history versus control soils (Fig. 3) was not associated with either competitive

367   response ($F_{1,25} = 0.07$, $r^2 = 0.003$, $P = 0.79$, $\lambda = 0.978$) or competitive effect ($F_{1,25} = 0.57$, $r^2 =$

368   0.022, $P = 0.45$, $\lambda = 0.266$).

369   Metrics of competitive ability were not strongly correlated across soil treatments.

370   Specifically, CR in control soil only explained 5.7% of the variation in CR in *A. petiolata* history

371   soil, and CE in control soil only explained 12% of the variation in CE in history soil (Fig. 6). CR

372   and CE were positively correlated in control soil ($F_{1,25} = 7.44$, $r^2 = 0.229$, $P = 0.01$, $\lambda = 1$), but

373   were not correlated with each other in history soil ($F_{1,25} = 2.73$, $r^2 = 0.098$, $P = 0.11$, $\lambda = 0$).

374

375   **Discussion**

376   Our results indicate that *A. petiolata* is a strong competitor against a range of common

377   mycorrhizal grassland, old field and forest species in soils which had no previous history with its

378   conspecifics, but contrary to expectation, this competitive advantage weakens in soil with a

379   history of conspecific growth. In uninvaded control soil, for example, *A. petiolata* suppressed the

380   biomass of a majority of competitor plant species by an average effect size that exceeded 50%

381   (Fig. 1). By contrast, the suppression of competitor species' biomass by *A. petiolata* was weaker

382   in history soil, with an effect size that was less than half of that observed in control soil.

383   Moreover, 70% of species responded negatively to the presence of *A. petiolata* in control soil,

384   but only 26% of species responded negatively in conspecific history soil. Because the soil history

385   treatment reduced plant available nutrients in soil and reduced mycorrhizal colonization of roots,

386   differences in *A. petiolata* competitive ability between treatments could be caused by these

387   factors acting independently or in combination. Nevertheless, our findings suggest that the

388   competitive ability of newly introduced *A. petiolata* is sufficient to displace competitor species in

389   previously uninvaded sites in the short term, but modification of the soil environment by *A.*

390   *petiolata* may not enhance its competitive ability.

391   The weaker competitive effect of *A. petiolata* on other species in history soil occurred

392   despite suppression of mycorrhizal fungi. Mycorrhizal colonization in soils with *A. petiolata*

393   history (Fig. 4) was reduced by levels comparable to that observed in the field (e.g., Barto et al.,

394   2011), with concomitant reductions in competitor plant growth (Fig. 3). However, competitor

395   species were still better able to resist competition from *A. petiolata* in soils with a history of the

396   invader than control soils. Though we cannot separate the individual effects of nutrient depletion

397   and reduced mycorrhizal colonization on the outcome of competition in the present study, we

398   note that *A. petiolata* was suppressed in the soil history treatment at a level that was more than

399   three times the average level of suppression across all competitor species (Fig. 3). Because *A.*

400   *petiolata* is nonmycorrhizal, the strong negative effect of growth in conspecific soil on its

401   biomass was most likely caused by lower nutrients. We suggest, therefore, that the most likely

402   explanation for weaker competitive ability of *A. petiolata* in history soils is that the negative

403   effect of nutrient depletion on *A. petiolata* was stronger than the negative effect of suppressing

404   mycorrhizal colonization on competitor species. Davis et al. (2012) also observed weak effects

405   of *A. petiolata* soil history on the biomass of competitor species. The observation that

406   competition was weaker overall in history soil is also consistent with the hypothesis that when

407   plant growth is suppressed by environmental stress or low fertility, limited overall demand for

408   resource uptake reduces the strength of competition (Grime 1977; Lamb et al. 2007).

409   Our findings imply that the negative effect of *A. petiolata* on mycorrhizal fungi as a

410   mechanism of competition during invasion may be weaker than previously expected. Though

411   this interpretation is supported by weaker competition in the *A. petiolata* history soil, where

412   colonization of roots by AM fungi was reduced, it is tentative for two reasons. First, we did not

413   quantify AM fungal colonization of roots for all competitor species, and it is possible that these

414   effects were not the same in unmeasured species. Second, though the reduction in AM fungal

415   colonization of roots is consistent with the presence of fungal inhibiting secondary chemicals

416   produced by *A. petiolata*, we did not directly quantify the concentration of these compounds in

417   *A. petiolata* history soil. Though secondary chemicals produced by *A. petiolata* likely reduced

418   fungal populations during the 5 month soil conditioning period (Roberts & Anderson, 2001;

419   Stinson et al., 2006), they may have been absent in the main experiment because of a short half-

420   life (Barto & Cipollini, 2009).

421   We hypothesized that *A. petiolata*'s strong competitive ability is caused by the capacity

422   to deplete limiting resources to levels lower than resident species, as expected from resource

423   competition theory (Tilman, 1988; Tilman & Wedin, 1991; Bever et al., 2010). However,

424   simulated nutrient depletion of soils by *A. petiolata* more strongly suppressed its own growth

425   relative to competitor species. The ability of *A. petiolata* to suppress other species may therefore

426   be caused by other traits, such as fast growth rate and high allocation to leaf area (Grime, 1977;

427   Funk et al., 2008; Engelhardt & Anderson, 2011). The tendency for decomposing *A. petiolata*

428   leaf litter to increase soil nutrient availability in the years following successful invasion (Rodgers

429   et al., 2008b) also suggests that this species has evolved to compete effectively at high, rather

430   than low, soil resources. In addition, we note that our experiment simulates competition between

431   first year individuals of *A. petiolata* and competitor species. In the field, competition also takes

432   place between spring flowering *A. petiolata* plants that have over wintered as rosettes and newly

433   germinating plants of competitor species, which can further advantage *A. petiolata* (Herold et al.,

434   2011). The observation that nutrient depletion caused by conspecifics reduces individual plant

435   performance, however, corroborates previous findings that *A. petiolata* experiences relatively

436   strong intra-specific competition (Meekins & McCarthy, 1999; Davis et al., 2012; Leicht-Young

437   et al., 2012), which would limit the net reproductive rate of established populations. The

438   possibility of nutrient-limitation mediated density-dependent population regulation is consistent

439   with recent demographic analyses showing that in situations where other biotic factors such as

440   herbivory are excluded, established *A. petiolata* populations decline towards extinction (Knight

441   et al., 2009; Kalisz et al., 2014).

442   Growth form was the best predictor of the ability of competitor species to either resist or

443   suppress *A. petiolata*, but this effect varied with soil history and competition metric. For

444   example, *A. petiolata* suppressed the growth of all three growth forms in control soil, but this

445   effect was more modest in *A. petiolata* history soil. By contrast, grasses suppressed invader

446   biomass in both soil treatments, whereas forbs had no effect, and trees appeared to facilitate the

447   growth of *A. petiolata* in control soils. The ability of grasses to suppress *A. petiolata* may have

448 occurred because they were taller than other growth forms at a young age, which would increase

449 light acquisition (Grime 1977; Gaudet & Keddy, 1988; Goldberg & Landa, 1991; Rosch et al.,

450 1997; Keddy et al. 2002; Wang et al. 2010). Grasses also had relatively fine roots (Fig. 5), which

451 would increase nutrient uptake capacity (Aerts et al., 1991; Goldberg, 1996; Casper & Jackson,

452 1997). Nonetheless, height may be the most important factor because grasses and forbs had

453 similar photosynthetic capacity and root architecture, yet forbs did not suppress *A. petiolata*

454 biomass. Meekins and McCarthy (1999) also found that *A. petiolata* was a weaker competitor

455 against tall relative to short species. Though the ability of *A. petiolata* to suppress tree growth

456 has been previously observed (Stinson et al., 2007), the observation that trees might facilitate *A.*

457 *petiolata* growth was unexpected. This effect may be due to aspects that were unique to the two

458 tree species, *P. strobus* and *T. occidentalis*, which had the strongest beneficial effect on *A.*

459 *petiolata*. These species were the only conifers in the sample and also ranked lowest in terms of

460 growth rate (Fig 1). The relatively strong growth form effects of competitor species on *A.*

461 *petiolata* we report here may not be universal however. Other studies suggest that trees can be

462 strong competitors (Meekins & McCarthy, 1999; Smith & Reynolds, 2014) and grasses can be

463 weak competitors (Smith & Reynolds, 2014) against *A. petiolata*.

464   Functional trait variation, beyond that associated with growth form, did not predict either

465 the ability of competitor species to resist suppression by, or their ability to suppress, *A. petiolata*.

466 When growth form was included in multiple regressions between traits and competitive response

467 or competitive effect, no significant relationships were found, regardless of soil treatment (Table

468 4). There was also limited trait plasticity in response to *A. petiolata* history in soil (Fig. 5),

469 despite strong effects on plant biomass. These findings are consistent with those of Wang et al.

470 (2010), who also reported weak relationships between trait values and competitive ability. The

471 inability to detect specific relationships between traits and competitive ability could be caused by

472 the possibility that competitive ability depends on combinations of several traits or traits that

473 were not measured (Wardle et al., 1998; Wang et al., 2010), or because functionally alternate

474   strategies, such as efficient resource acquisition or resource storage, can result in similar

475   competitive abilities (Grime, 1977).

476   Our findings have implications for recent hypotheses about how competitive response

477   and competitive effect should be correlated across environments (Keddy et al., 1994; Keddy et

478   al., 2002; Wang et al., 2010). Specifically, competitive response is expected to be context

479   specific, varying with resource availability or other ecological and environmental factors, and is

480   not expected to be correlated across environments. By contrast, competitive effect is expected to

481   be a general property of a species, such that it is positively correlated across environments

482   (Wang et al., 2010). Our results are generally consistent with these predictions (Fig. 6), but the

483   relationship between competitive effect in control and history soils was weaker than (i.e., $r^2 =$

484   0.12, Fig. 6b) found in other studies (Keddy et al., 1994; Keddy et al., 2002; Wang et al., 2010).

485   Observing such context dependency in the competitive effect of *A. petiolata* was not unique to

486   our study. For example, Smith & Reynolds (2014) found that *A. petiolata* could suppress other

487   species under high light conditions, but had much weaker effects in the shade. Our findings

488   suggest the ability of competitor species to either resist suppression by, or suppress, *A. petiolata*

489   cannot be confidently predicted from one ecological context to another.

490   In conclusion, our findings suggest that *A. petiolata* has the potential to displace resident

491   species in a community upon initial invasion via a relatively strong competitive ability.

492   However, its competitive ability is weakened, rather than strengthened, by conspecific soil

493   history effects. Like previous studies, we observed that soil with a history of *A. petiolata* reduces

494   the ability of mycorrhizal fungi to colonize the roots of competitor species. However, this

495   negative novel weapons effect on mycorrhizal plant species did not appear overcome the

496   negative history effects of soil nutrient depletion on *A. petiolata*. These findings suggest that the

497   inhibitory potential of *A. petiolata* on competitor species via mycorrhizal suppression may not be

498   as strong as previously suggested. In addition, because longer term effects of *A. petiolata*

499   invasion include an overall increase in plant available soil nitrogen and phosphorus (Rodgers et

500   al., 2008b), mycorrhizal suppression is unlikely to be a strong mechanism of competition in the

501 years following invasion. This is because the effect of losing the fungal symbiont approaches

502 neutrality when mycorrhizal plants are grown with supplemental nutrients (Hoeksema et al.,

503 2010; Johnson 2010). The potential for weak mycorrhizal suppression effects suggests that

504 eradication or control measures based on minimizing novel biochemical weapons effects in *A.*

505 *petiolata* may be less successful than other approaches. As suggested by other studies, reducing

506 propagule pressure by removal of flowering individuals (Herold et al., 2011; Phillips-Mao et al.,

507 2014) and suppressing browsing by deer (Kalisz et al., 2014) could be more effective strategies

508 to counteract the invasion of *A. petiolata* in North America.

509

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698 **Figure Legends**

699 Figure 1. Biomass of competitor species in response to competition with *A. petiolata* in control

700 (A) or soil with a history of *A. petiolata* (B). Biomass within each growth form are shown in the

701 insets. Black bars indicate plants grown alone and grey bars indicate plants grown in competition

702 with *A. petiolata*. Statistically significant differences were determined using planned orthogonal

703 1-df contrasts, and are indicated with an asterisk.

704

705 Figure 2. Biomass of *A. petiolata* alone or in response to competition with other species in

706 control (A) or soil with a history of *A. petiolata* (B). Biomass of *A. petiolata* alone versus in

707 competition with members of different growth forms are shown in the insets. Statistically

708 significant differences were determined using planned orthogonal 1-df contrasts, and are

709 indicated with an asterisk.

710

711 Figure 3. The log response ratio of plant biomass without competition in *A. petiolata* history

712 relative to control soil. Statistically significant differences between soil treatments were

713 determined using planned orthogonal 1-df contrasts, and are indicated with an asterisk.

714

715 Figure 4. The effect of soil history with *A. petiolata* on the colonization of roots by arbuscular

716 mycorrhizal (AM) hyphae (A) AM arbuscules (B), and vesicles (C). Statistically significant

717 differences between soil treatments are indicated with an asterisk.

718

719 Figure 5. The effect of growth form and exposure to either control or *A. petiolata* soil history on

720 quantum yield of PSII at weeks 5 and 9 (A), leaf chlorophyll concentration at weeks 5 and 9 (B)

721 and plant height at week 5 (C). The effect of growth form on root diameter (D) and specific root

722 length (E). Different letters above bars, when present, represent statistically significant

723 differences ($P < 0.05$) among groups within each treatment, as determined by a comparison of

724 95% confidence limits among groups.

725

726   Figure 6. Relationships between competitive response (A) or competitive effect (B) across

727   control and *A. petiolata* history soils.

1

Figure 1

Figure 1. Biomass of competitor species in response to competition with *A. petiolata* in control (A) or soil with a history of *A. petiolata* (B). Biomass within each growth form are shown in the insets. Black bars indicate plants grown alone and grey bars indicate plants grown in competition with *A. petiolata*. Statistically significant differences were determined using planned orthogonal 1-df contrasts, and are indicated with an asterisk.

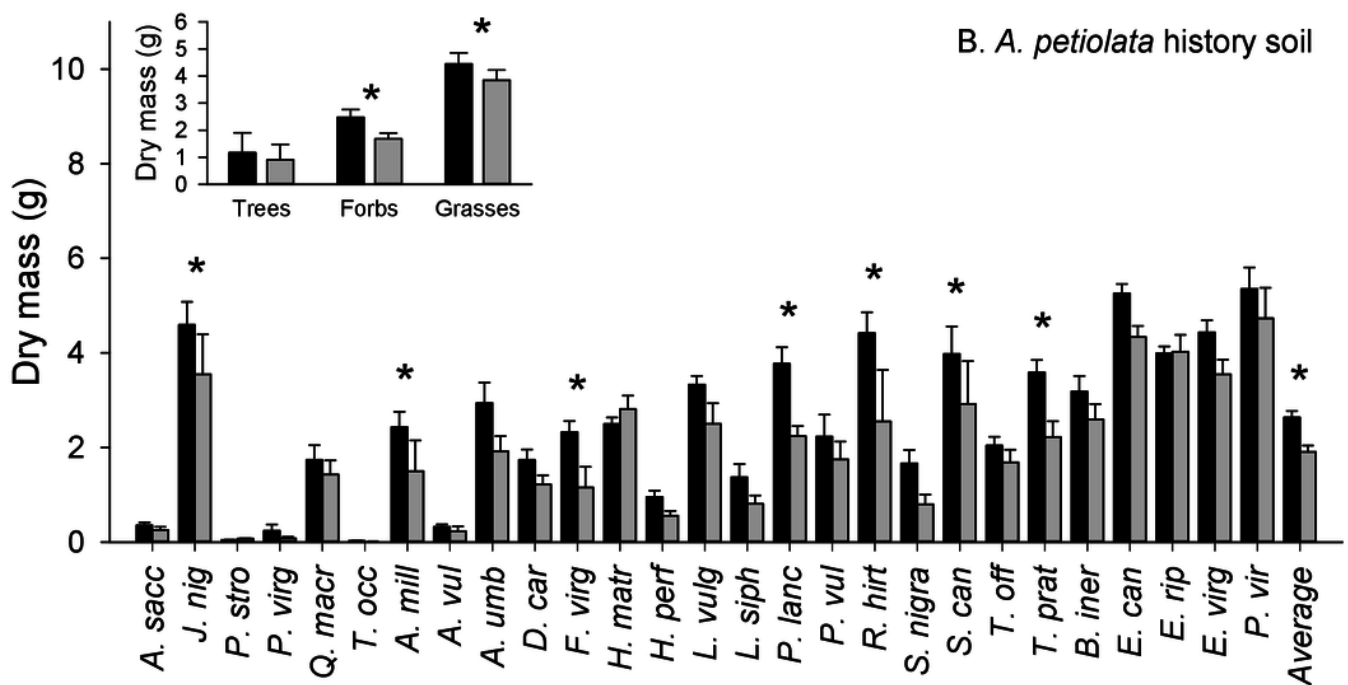
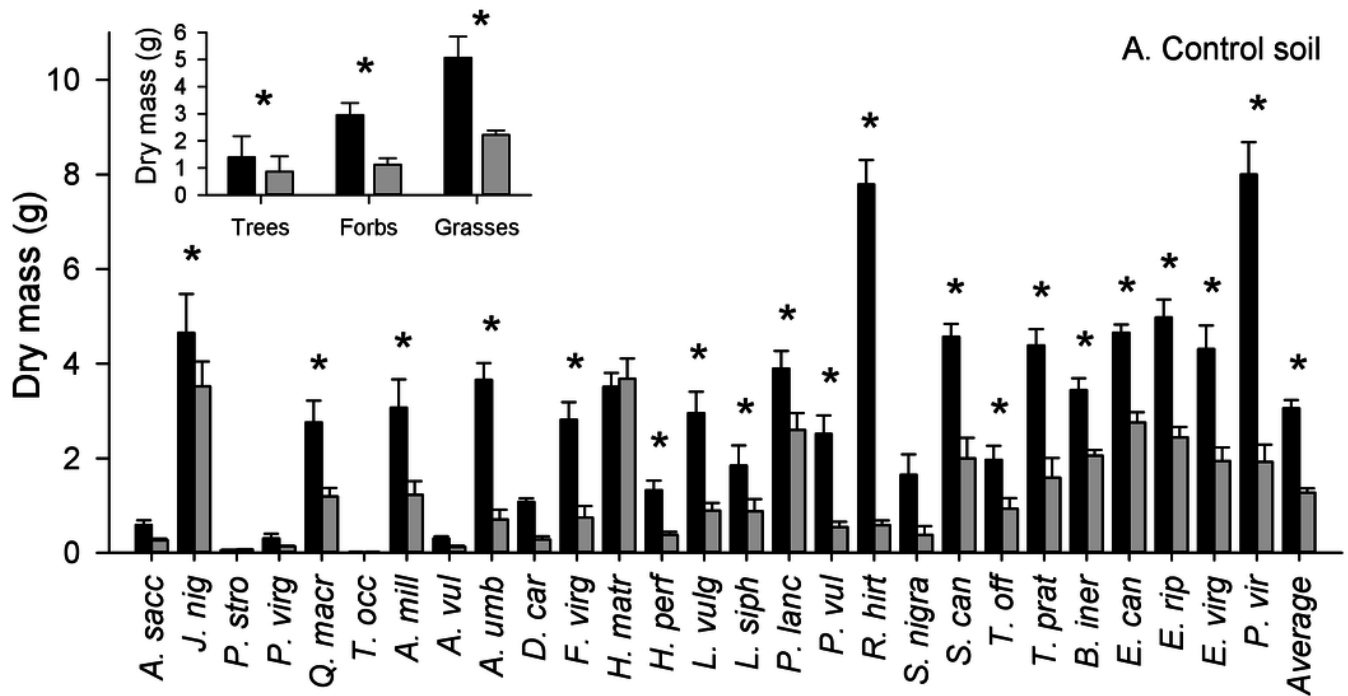



Figure 2

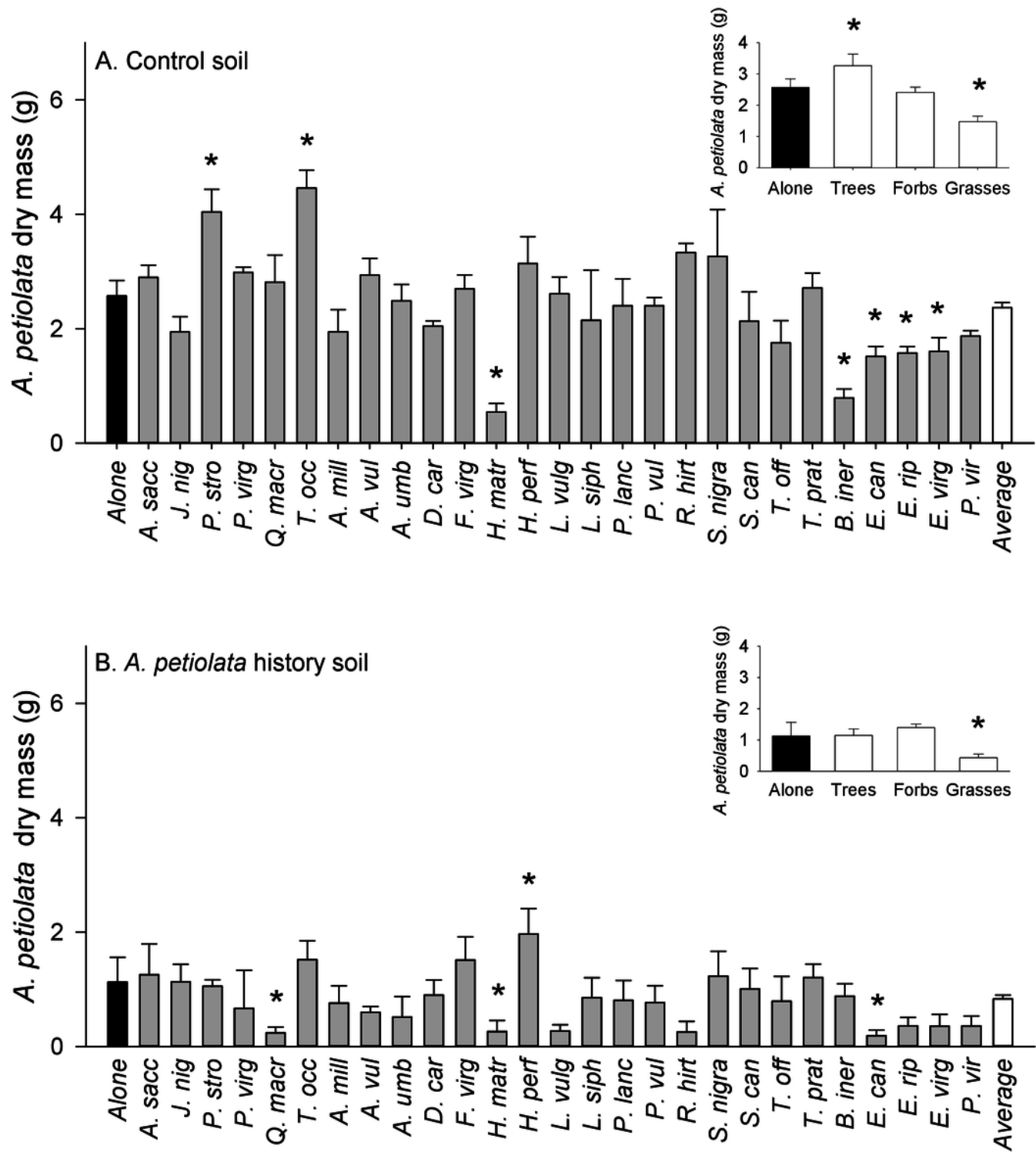
Figure 2. Biomass of *A. petiolata* alone or in response to competition with other species in control (A) or soil with a history of *A. petiolata* (B). Biomass of *A. petiolata* alone versus in competition with members of different growth forms are shown in the insets. Statistically significant differences were determined using planned orthogonal 1-df contrasts, and are indicated with an asterisk.

3

Figure 3

Figure 3. The log response ratio of plant biomass without competition in *A. petiolata* history relative to control soil. Statistically significant differences between soil treatments were determined using planned orthogonal 1-df contrasts, and are indicated with an asterisk.

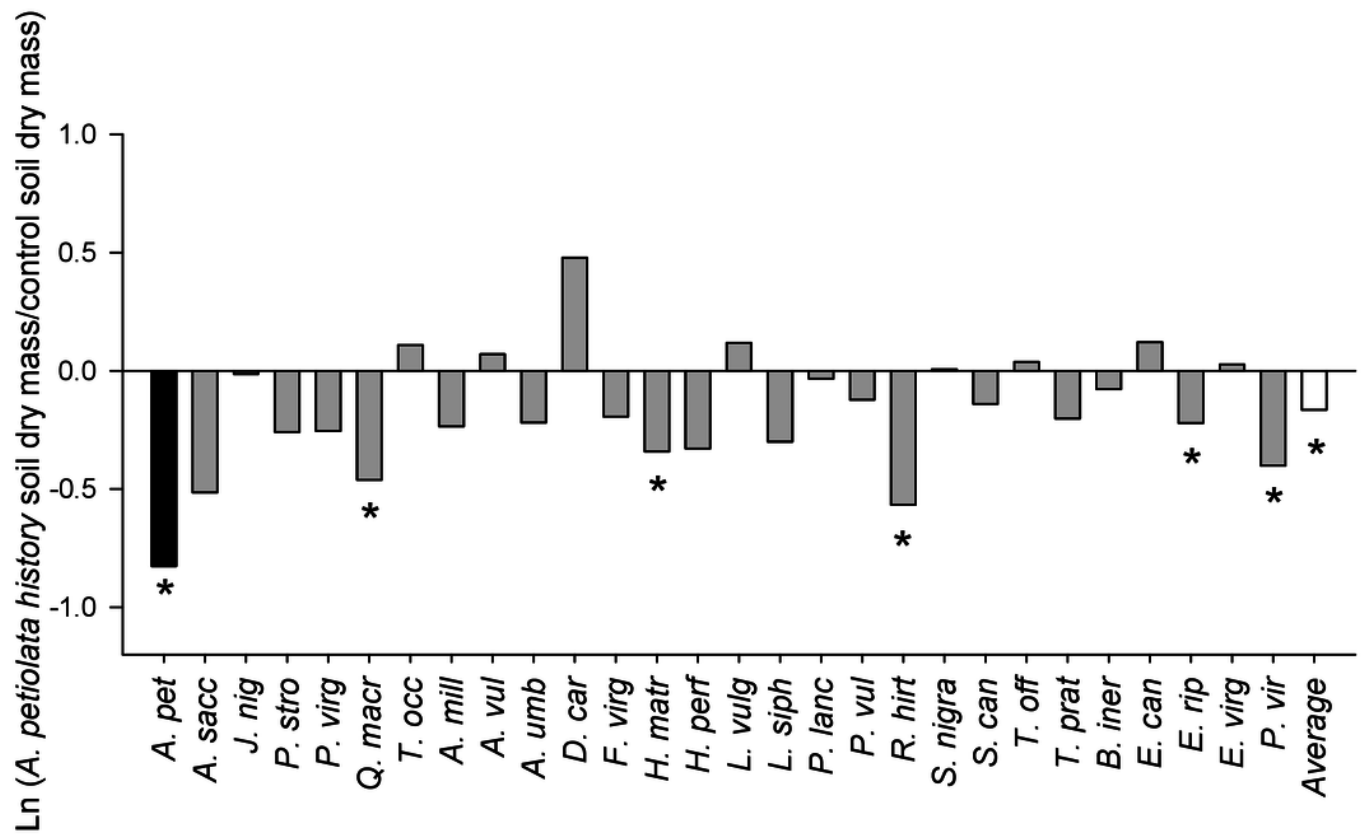



Figure 4

Figure 4. The effect of soil history with *A. petiolata* on the colonization of roots by arbuscular mycorrhizal (AM) hyphae (A) AM arbuscules (B), and vesicles (C). Statistically significant differences between soil treatments are indicated with an asterisk.

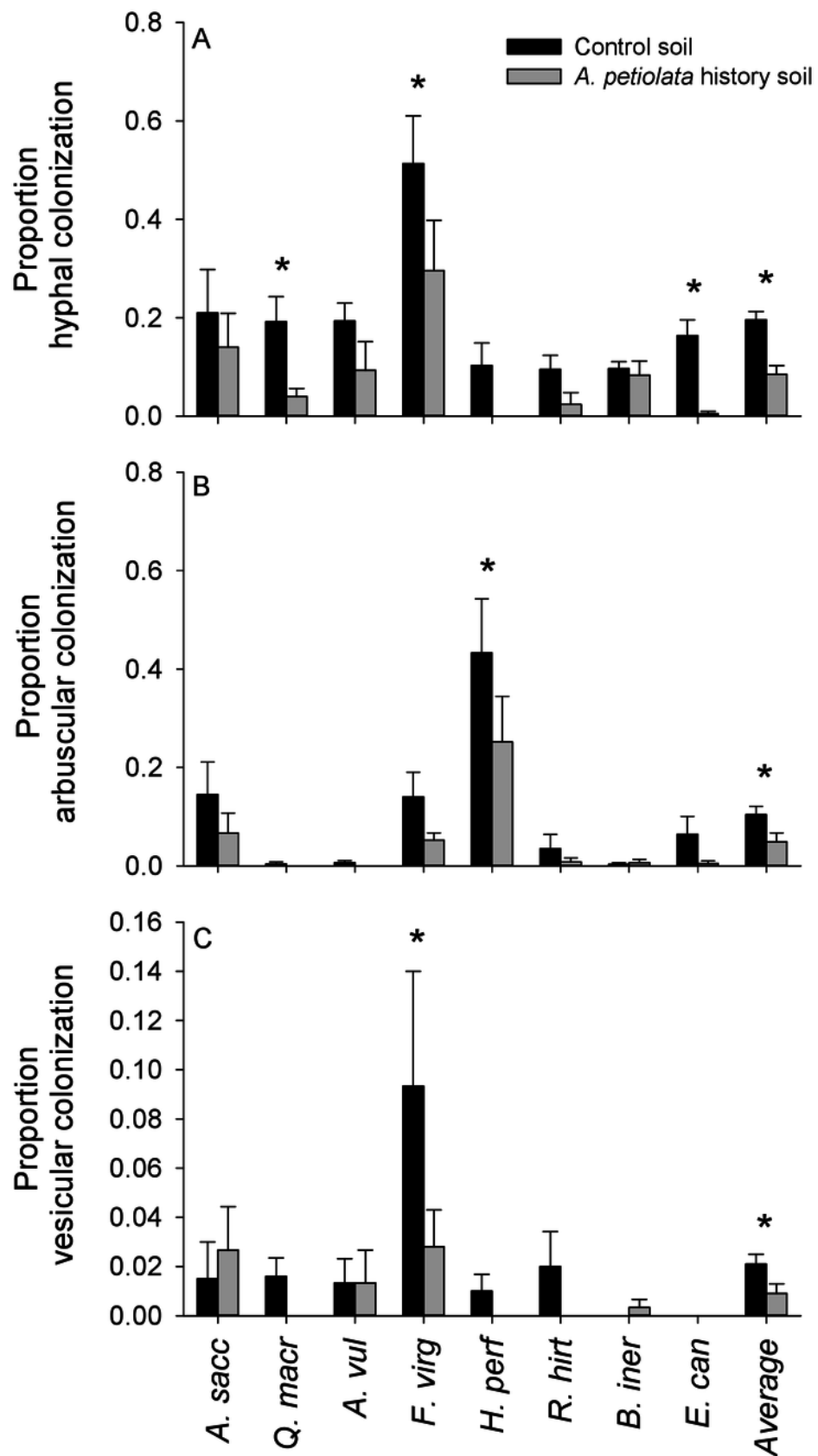



Figure 5

Figure 5. The effect of growth form and exposure to either control or *A. petiolata* soil history on quantum yield of PSII at weeks 5 and 9 (A), leaf chlorophyll concentration at weeks 5 and 9 (B) and plant height at week 5 (C). The effect of growth form on root diameter (D) and specific root length (E). Different letters above bars, when present, represent statistically significant differences (P < 0.05) among groups within each treatment, as determined by a comparison of 95% confidence limits among groups.

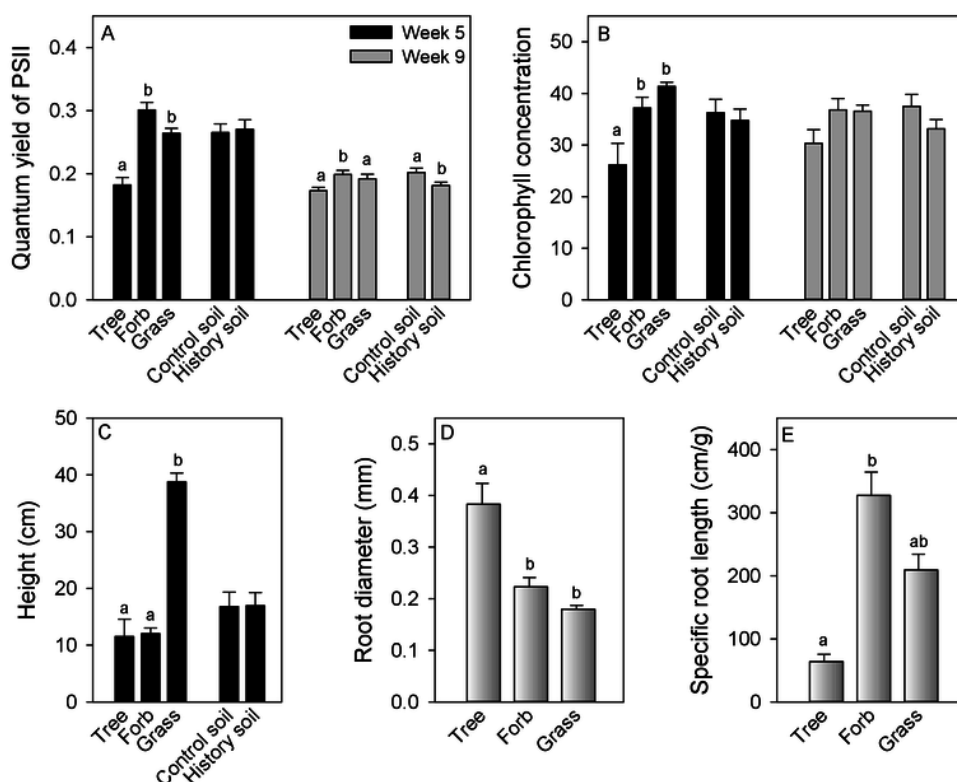



Figure 6

Figure 6. Relationships between competitive response (A) or competitive effect (B) across control and *A. petiolata* history soils.

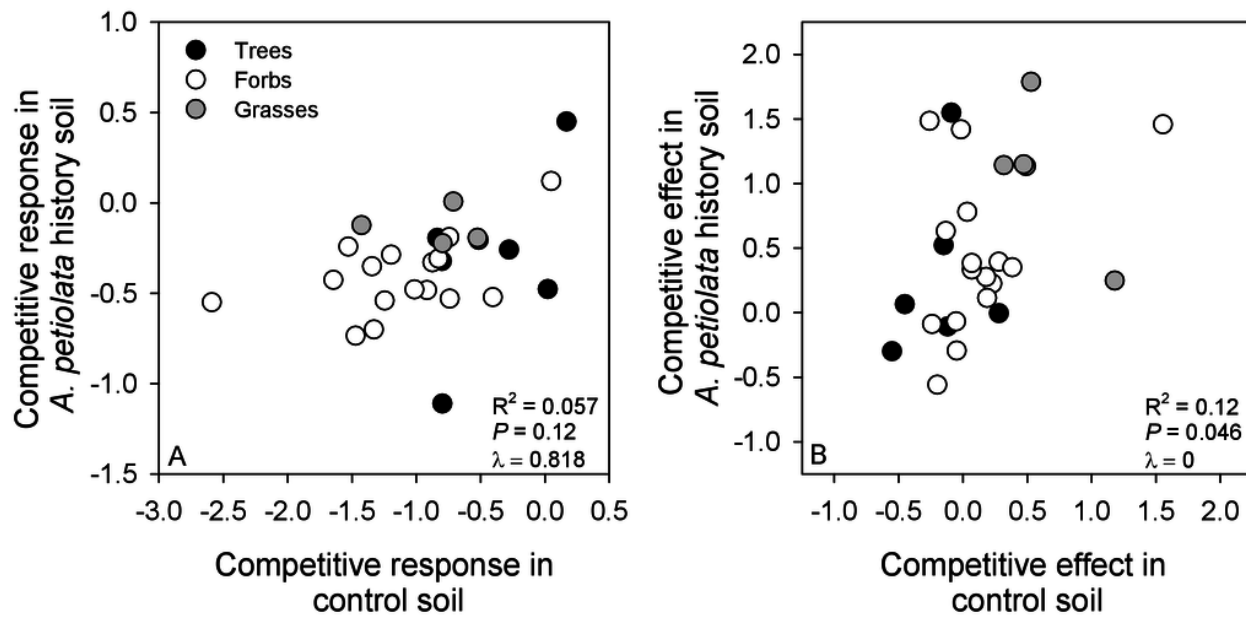



Table 1

Table 1. List of competitor species used in the study, along with information on their plant family affiliation, growth form, status in North America (18 native, 9 introduced), and whether plants are arbuscular mycorrhizal (AM), ecto-mycorrhizal (ECM), or ambiguous (both mycorrhizal and non-mycorrhizal states reported in the literature). Mycorrhizal state was determined from Wang & Qiu (2006). Seeds were obtained from [A]Acorus Restoration, [B]Angelgrove Seed Company, [C]Ontario Tree Seed Facility [D]Richters Herbs, or field collections from the [E]University of Guelph Arboretum.

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6   Herbs, or field collections from the [E]University of Guelph Arboretum.

Latin name	Family	Growth Form	Status	Mycorrhizal State
[1]*Acer saccharum* L.	Aceraceae	Tree	Native[C]	AM
[1]*Juglans nigra* L.	Juglandaceae	Tree	Native[C]	AM
[2]*Pinus strobus* L.	Pinaceae	Tree	Native[C]	ECM
[1]*Prunus virginiana* L.	Rosaceae	Tree	Native[C]	AM
[2]*Quercus macrocarpa* Michx.	Fagaceae	Tree	Native[C]	ECM
[1]*Thuja occidentalis* L.	Cupressaceae	Tree	Native[C]	AM
[1]*Achillea millefolium* L.	Asteraceae	Perennial Forb	Native[D]	AM
[1]*Aquilegia vulgaris* L.	Ranunculaceae	Perennial Forb	Introduced[D]	AM
[1]*Aster umbellatus* Miller	Asteraceae	Perennial Forb	Native[D]	AM
[1]*Daucus carota* L.	Apiaceae	Biennial Forb	Introduced[E]	AM
[1]*Fragaria virginiana* Miller.	Rosaceae	Perennial Forb	Native[B]	AM
[3]*Hesperis matronalis* L.	Brassicaceae	Biennial Forb	Introduced[A]	Ambiguous
[1]*Hypericum perforatum* L.	Clusiaceae	Perennial Forb	Introduced[A]	AM
[1]*Leucanthemum vulgare* Lam.	Asteraceae	Perennial Forb	Introduced[A]	AM
[1]*Lobelia siphilitica* L.	Campanulaceae	Perennial Forb	Native[A]	AM
[1]*Plantago lanceolata* L.	Plantaginaceae	Perennial Forb	Introduced[D]	AM
[1]*Prunella vulgaris* L.	Lamiaceae	Perennial Forb	Native[B]	AM
[1]*Rudbeckia hirta* L.	Asteraceae	Perennial Forb	Native[B]	AM
[3]*Sambucus nigra spp. canadensis* L.	Caprifoliaceae	Perennial Forb	Native[A]	Ambiguous
[1]*Solidago canadensis* L.	Asteraceae	Perennial Forb	Native[E]	AM

[1]*Taraxacum officinale* F.H. Wigg.	Asteraceae	Perennial Forb	Introduced[B]
[1]*Trifolium pratense* L.	Fabaceae	Biennial Forb	Introduced[E]
[1]*Bromus inermis* Leyss.	Poaceae	Perennial Grass	Introduced[E]
[1]*Elymus canadensis* L.	Poaceae	Perennial Grass	Native[B]
[1]*Elymus riparius* Wiegand.	Poaceae	Perennial Grass	Native[B]
[1]*Elymus virginicus* L.	Poaceae	Perennial Grass	Native[B]
[1]*Panicum virgatum* L.	Poaceae	Perennial Grass	Native[A]

Table 2

Table 2. A three-way ANOVA table describing the effects of species identity, competition with

A. petiolata, soil history and their interactions on dry mass of competitor species.

1   Table 2. A three-way ANOVA table describing the effects of species identity, competition with *A. petiolata*, soil history and their

2   interactions on dry mass of competitor species.

Source	Type III Sums of Squares	df	Mean Square	*F*	*P*
Species	1141.51	26	43.90	66.78	5.29×10^{-144}
Soil history	1.41	1	1.41	2.14	0.144
Competition	209.97	1	209.97	319.38	1.57×10^{-55}
Species * Soil history	32.20	26	1.24	1.88	0.006
Species * Competition	141.18	26	5.43	8.26	1.76×10^{-25}
Soil history* Competition	45.14	1	45.14	68.65	1.10×10^{-15}
Species * Soil history* Competition	68.44	26	2.63	4.00	4.42×10^{-10}
Error	326.75	497	0.66		

Table 3

Table 3. A two-way ANOVA table describing the effects of competitor species identity, soil history and their interaction on the dry mass of *A. petiolata*.

2   Table 3. A two-way ANOVA table describing the effects of competitor species identity, soil history and their interaction on the dry

3   mass of *A. petiolata*.

Source	Type III Sums of Squares	df	Mean Square	F	P
Species	92.4	26	3.55	6.76	3.74×10^{-17}
Soil history	179.59	1	179.59	341.39	9.51×10^{-48}
Species * Soil history	40.37	26	1.55	2.95	7.30×10^{-06}
Error	124.15	236	0.53		

Table 4

Table 4 Partial correlation coefficients (β) indicating relationships between competitive response (CR) or competitive effect (CE) in control or history soil, and plant functional traits, including height at 5 weeks, quantum yield of PS II in the light [Y(II)] at 5 and 9 weeks, leaf chlorophyll content at 5 and 9 weeks, mean root diameter and specific root length (SRL). Because traits differed between trees, forbs and grasses, plant growth form was included as a covariate in the analysis, but only β and significance values for traits are shown. The degree to which residuals from the multiple regression were correlated with phylogeny is indicated by λ.

1 Table 4. Partial correlation coefficients (β) indicating relationships between competitive response (CR) or competitive effect (CE) in
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4 trees, forbs and grasses, plant growth form was included as a covariate in the analysis, but only β and significance values for traits are
5 shown. The degree to which residuals from the multiple regression were correlated with phylogeny is indicated by λ.

Dependent variable	Trait	β	P	Dependent variable	Trait	β	P
CR control soil	Height @ 5 wks	-0.12	0.59	CR history soil	Height @ 5 wks	-0.09	0.70
$\lambda = 0$	Y(II) @ 5 wks	0.023	0.92	$\lambda = 1$	Y(II) @ 5 wks	0.42	0.06
	Y(II) @ 9 wks	0.18	0.44		Y(II) @ 9 wks	0.082	0.72
	Chl @ 5 wks	-0.040	0.86		Chl @ 5 wks	0.080	0.73
	Chl @ 9 wks	0.053	0.82		Chl @ 9 wks	-0.16	0.49
CE control soil	Height @ 5 wks	-0.02	0.93	CE history soil	Height @ 5 wks	0.064	0.78
$\lambda = 0$	Y(II) @ 5 wks	0.27	0.24	$\lambda = 0$	Y(II) @ 5 wks	0.063	0.79
	Y(II) @ 9 wks	-0.11	0.64		Y(II) @ 9 wks	0.050	0.83
	Chl @ 5 wks	0.061	0.79		Chl @ 5 wks	-0.12	0.61
	Chl @ 9 wks	0.11	0.63		Chl @ 9 wks	0.25	0.27
CR control soil	Root diameter	-0.23	0.28	CR history soil	Root diameter	-0.11	0.61
$\lambda = 0$	SRL	0.09	0.67	$\lambda = 0.981$	SRL	-0.13	0.57
CE control soil	Root diameter	-0.35	0.11	CE history soil	Root diameter	-0.22	0.32
$\lambda = 1$	SRL	-0.10	0.64	$\lambda = 0$	SRL	-0.23	0.30