Belowground competition drives invasive plant impact on native species regardless of nitrogen availability

Arthur A.D. Broadbent[1*], Carly J. Stevens[1], Duane A. Peltzer[2], Nicholas J. Ostle[1] and Kate H. Orwin[2]

1 - Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YW, UK

2 - Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

*Corresponding author, orchid id: orcid.org/0000-0002-8438-7163;

Email: a.broadbent2@lancaster.ac.uk

Tel: +44 (0)7549 689932

Author contributions: AB and CS conceived the experiment; AB conducted the experiment and data analysis; DP coordinated fieldwork; AB, CS, DP, NO and KO designed experiments and wrote the manuscript.

Abstract

Plant invasions and eutrophication are pervasive drivers of global change that cause biodiversity loss. Yet, how invasive plant impacts on native species, and the mechanisms underpinning these impacts, vary in relation to increasing nitrogen (N) availability remains unclear. Competition is often invoked as a likely mechanism, but the relative importance of the above and belowground components of this is poorly understood, particularly under differing levels of N availability. To help resolve these issues, we quantified the impact of a globally invasive grass species, *Agrostis capillaris*, on two co-occurring native New Zealand grasses, and vice versa. We explicitly separated above and belowground interactions amongst these species experimentally and incorporated an N addition treatment. We found that competition with the invader had large negative impacts on native species growth (biomass decreased by half), resource capture (total N content decreased by up to 75%) and even nutrient stoichiometry (native species tissue C: N ratios increased). Surprisingly, these impacts were driven directly and indirectly by belowground competition, regardless of N availability. Higher root biomass likely enhanced the invasive grass's competitive superiority belowground, indicating that root traits may be useful tools for understanding invasive plant impacts. Our study shows that belowground competition can be more important in driving invasive plant impacts than aboveground competition in both low and high fertility ecosystems, including those experiencing N enrichment due to global change. This can help to improve predictions of how two key drivers of global change, plant species invasions and eutrophication, impact native species diversity.

Introduction

The rapid increases in plant species invasions and soil nitrogen (N) availability are major drivers of global change and biodiversity loss (Vitousek et al. 1997; Stevens et al. 2004; Vilà et al. 2011; Seabloom et al. 2015; Van Kleunen et al. 2015). However, how increasing N availability alters invasive species impacts on native species, and the mechanisms underlying those impacts, remains uncertain. A stronger mechanistic understanding of invasive plant impacts under varying edaphic conditions would enable better prediction of where and when impacts on native species are most likely to occur. In turn, this could facilitate pre-emptive management to prevent negative impacts, thereby protecting native species diversity and ultimately, reducing global biodiversity loss.

Interspecific competitive interactions are often proposed as the primary pathway for invasive plant impacts, yet few studies experimentally test whether, or which, competitive mechanisms underlie invader impacts (Levine et al. 2003; Seabloom et al. 2003; Tylianakis et al. 2008; Barney et al. 2013, 2015). For example, the relative importance of above and belowground competitive interactions in determining invasive plant species impacts is unclear. Further uncertainty arises from the likely shifts in importance of different impact mechanisms, such as above and belowground competition, following increases in soil nutrient availability. We found only two experiments that explicitly separated above and belowground competitive interactions between native and invasive species and both reported that belowground competition was more important in delivering invader impacts (Dillenburg et al. 1993; Kueffer et al. 2007). However, other lines of evidence suggest aboveground competition may also be a strong driver, particularly following increases in nutrient availability (Tilman 1982; Cahill 1999; Hautier et al. 2009; Borer et al. 2014). Indeed, increased soil fertility can increase the competitive superiority of invasive plants (Daehler 2003; Besaw et al. 2011), which tend to have more exploitative traits than co-occurring native

50 species (Leishman et al. 2007; van Kleunen et al. 2010; Ordonez et al. 2010). These traits

51 should be advantageous under high resource conditions and in competing for light, although

52 evidence for this is mixed (Leishman et al. 2010; Ordonez and Olff 2013). Furthermore, the

53 invasive plant species with the most exploitative aboveground traits tend to have the greatest

54 negative impact on native species (Lai et al. 2015). It is therefore likely that both above and

55 belowground competition can underpin invasive species impacts and that it depends on

56 belowground resource availability, yet experiments that test this explicitly remain remarkably

57 rare.

58 Increasing N availability to increase productivity is common practice in grasslands, where

59 invasion rates are among the highest worldwide (Firn et al. 2011). Additionally, co-occurring

60 invasive and native grass species are often closely related and functionally similar.

61 Grasslands thus constitute ideal model systems in which to test the importance of above and

62 belowground competition as mechanisms of invasive plant impacts across varying levels of

63 soil N availability. One such system is low-fertility New Zealand grassland that is designated

64 as valuable conservation habitat (Mark and McLennan 2005; Rose and Frampton 2007).

65 These grasslands are experiencing widespread declines in native species diversity (Duncan et

66 al. 2001) associated with non-native grass invasions (Rose et al. 2004) and increases in

67 nitrogen (N) availability (Scott 2000; Dickie et al. 2014). Invasive grasses in New Zealand,

68 and elsewhere, tend to have more exploitative traits than co-occurring native grasses (Craine

69 and Lee 2003; Wilsey and Polley 2006), suggesting that invasive grasses may be superior

70 aboveground competitors compared to native grasses (Johnson et al. 2008; Lai et al. 2015).

71 Their aboveground competitive superiority is likely to increase following increases in soil N

72 availability, as this would lead to N no longer being a limiting resource, thereby allowing

73 competition to shift aboveground for light (Wilson and Tilman 1991; Aerts 1999), as has

74 been observed in various grasslands worldwide (Tilman 1988; Bobbink 1991; Hautier et al.

75 2009). However, as far as we are aware, there are no experiments that test this idea by

76 explicitly separating above and belowground competition across varying levels of N. To

77 address this, we test the following specific hypotheses:

78   1. Competition between invasive and native grass species benefits the invasive species,

79   *Agrostis capillaris* L., and decreases native species, *Poa cita* Edgar and *Poa colensoi*

80   Hook.f., growth and resource capture, compared with intraspecific competition;

81   2. *A. capillaris'* competitive impacts on native species, and the relative importance of

82   aboveground competition over belowground competition, both increase with

83   increasing N availability.

84

85 **Methods**

86 EXPERIMENTAL DESIGN AND GREENHOUSE CONDITIONS

87 We determined the effects of above- and belowground competition of a globally invasive

88 grass, *A. capillaris*, on two common perennial C_3 tussock grasses native to New Zealand: *P.*

89 *cita* and *P. colensoi*. *A. capillaris* is a Eurasian rhizomatous perennial C_3 grass species (height

90 = 20-70 cm) that is one of the most widespread invasive grasses in New Zealand (Edgar and

91 Forde 1991; Craine and Lee 2003; CABI 2017) and is also a pervasive weed in North

92 America, Australia and parts of South America (CABI 2017). It is a habitat generalist that

93 occurs across a wide range of climatic and edaphic conditions in its native and introduced

94 ranges (CABI 2017). These include Atlantic and continental climates at low and high

95 altitudes, along with low fertility, usually acidic, soils, as well as nutrient rich meadows (Hill

96 et al. 1999; Olde Venterink and Güsewell 2010; CABI 2017). *P. colensoi* (height = 5-30 cm)

97 and *P. cita* (height = 30-100 cm) are both short tussock grass species, widespread throughout

98   New Zealand, usually on low fertility acidic soils in montane areas (Daly 1964; Edgar and

99   Connor 2000). Our species were con-familiar and from the same functional group, which

100 controlled for confounding effects due to lifeform (Vila and Weiner 2004). Seeds of all

101 species were sourced from NZ populations by Speciality Seeds and Home Creek Nursery.

102 Treatments consisted of a full factorial cross of two native species identities (*P. cita* and *P.*

103 *colensoi*), four competition types (*control or full intraspecific competition, aboveground*

104 *competition, belowground competition and full competition*; Fig. 1) and two N addition

105 treatments (*control or "low N" and N-addition or "high N"*); with five replicates this made a

106 total of 80 pots. For each native - invasive species combination, two individuals of the native

107 species and two individuals of the invasive species were planted into 1 L pots. To minimise

108 lateral escape from competition, pots were surrounded by a 1 mm nylon mesh that was 10 cm

109 high. In order to separate above- and belowground competition, the pots were split using

110 solid PVC dividers within the pot, sealed with PVC glue and silicon, and opaque plastic

111 dividers above the pot. By varying the alignment of these dividers, four competition

112 treatments were created: 1) *control or intraspecific competition*, where plants were competing

113 with conspecifics above- and belowground; 2) *aboveground* and 3) *belowground*, where

114 plants were either competing with heterospecifics aboveground and conspecifics

115 belowground, or vice versa, respectively; and 4) *full competition*, where plants were

116 competing with heterospecifics above- and belowground (Fig. 1). Treatments were placed in

117 a randomised block design and blocks were rotated weekly. Our replacement design thus kept

118 plant density constant both overall and in each component of the pot (Fig. 1). This design

119 compares the effect of intraspecific competition with interspecific competition, which is

120 sometimes criticised due to the lack of a "zero" competition control, where plants are grown

121 without neighbours. However, invaded grassland communities often become relatively space

122 limited in the absence of a disturbance; therefore in field conditions, it is more likely for

123   plants to encounter neighbours. For this reason, our design was arguably more realistic than

124   an additive design, which involves zero competition treatments and inconsistent plant

125   densities.

126   Nitrogen addition treatment consisted of 133 mg NH_4NO_3 pot^{-1} $week^{-1}$ dissolved in 180 mL

127   de-ionised water, applied evenly over the area of each pot thrice weekly in 60 mL doses.

128   Nitrogen was used to increase resource availability as it is commonly used as an agricultural

129   fertiliser in grasslands. Soil N availability also increases in New Zealand grasslands

130   following invasion and removal of exotic woody species such as *Cytisus scoparius L.* and

131   *Pinus contorta* Douglas (Dickie et al. 2014; Broadbent et al. 2017). This is often followed by

132   exotic grass invasions, including *A. capillaris* (Williams 1998; Dickie et al. 2014), and so

133   might be a mechanism driving invasive success. Our rate of N addition is in line with net soil

134   N-mineralisation rates of grasslands in NZ that have been cleared of invasive N-fixing shrubs

135   (Broadbent et al. 2017).

136   Pots were filled with a mixture of field soil and autoclaved sand (3:1 by volume) to improve

137   drainage. Field soil was collected (depth = 10 cm) from 40 random locations of grassland-

138   shrubland habitat in St. James Conservation Area in New Zealand (Lat. Long. = -42.460273,

139   172.830938). Vegetation at the site consisted of a mixture of native and exotic species,

140   including those used in our study. Soil was sieved (4 mm) and homogenised prior to mixing

141   with sand. Mean pot soil pH (1: 2.5, soil: water) was 6.82 ± 0.02 (mean ± one SE), mean KCl

142   extractable N concentration (NO_3^{-}-N and NH_4^{+}-N) was 2.97 ± 0.15 μg N g $soil^{-1}$ and mean

143    $NaCO_3$ extractable PO_4^{-}-P concentration (Olsen-P) was 4.95 ± 0.29 μg P g $soil^{-1}$. The soils in

144   our study had low inorganic N concentrations (2.97 ± 0.15 μg N g $soil^{-1}$) and low N: P ratios

145   (0.6). These concentrations were determined colorimetrically in a segmented flow stream

146   using an AutoAnalyser (Seal-Analytical).

147   Plants were germinated in potting compost under the same standardised climatic conditions

148   that were used throughout the experiment: lighting regime: Light: Dark 16h: 8h, Temp

149   maximum: minimum 22 $^{\circ}$C: 16 $^{\circ}$C. After germination, seedlings were carefully transferred

150   into plugs, then two weeks later into pots, on the 21st June 2016. The mean mass of seedlings

151   did not differ between species prior to transplanting into pots (F = 2.1, p = 0.13, one-way

152   ANOVA). This was determined by harvesting, drying (65 $^{\circ}$C for 48 hours) and weighing ($\pm$

153   0.0001 g) the above- and belowground biomass of a random subset of 20 seedlings of each

154   species at the start of the experiment.

155   Plants were watered equally each day with ca. 100 mL of tap water per pot. The experiment

156   lasted 11 weeks, with all biomass harvested on the 6th September 2016. Biomass from each

157   pot was separated by species and dried at 65 $^{\circ}$C for 48 hours after all soil had been washed

158   from roots. Roots of individuals that were competing belowground were carefully separated.

159   Due to the difficulty of separating roots between species, this was only done for one side of

160   the division in each pot; the biomass value obtained was doubled to give an estimate per

161   species per pot. Biomass was separated into above and belowground components, with

162   aboveground components further separated into live and dead biomass, before being weighed

163   to 0.0001 g.

164   MEASUREMENTS AND CALCULATIONS

165   After weighing biomass, belowground and aboveground plant C and N concentrations were

166   measured on ground samples using an automated Dumas procedure on a Vario EL analyser

167   (Elementar). This was used to calculate whole plant mean C: N ratio (the mean of above- and

168   belowground C: N ratios). Since plant tissue C: N ratio is the mass of C relative to the mass

169   of N in plant tissue, it provides a similar measure to tissue %N content, with the advantage of

170   being easily compared to other substrates such as soil. To calculate total N content (g), %N

171 content of above- and belowground biomass components was multiplied by the

172 corresponding biomass (g) and then summed. We also calculated % dead aboveground

173 biomass (of total aboveground biomass) and two allocation patterns: root mass fraction

174 (RMF: belowground biomass/ total biomass) and root nitrogen fraction (RNF: belowground

175 N/ total N).

176 STATISTICAL ANALYSIS

177 We determined the effect of competition with invasive species on native species growth and

178 resource capture (hypothesis 1), and whether competition type and N addition modified this

179 effect (hypothesis 2), by using three-way ANOVAs on native species responses. The

180 responses we tested were mean total, aboveground and belowground biomass (g), mean dead

181 aboveground biomass (%), mean total N content (g), mean C: N ratio, mean RMF and mean

182 RNF. Each ANOVA had native species identity (*P. cita* or *P. colensoi*), competition

183 treatment (*control, aboveground, belowground* or *full*), N addition treatment (*low-N* or *high-*

184 *N*) and all interactions as factors. We also determined the effect of native species competition

185 on invasive species growth and resource capture (hypothesis 1), and whether this differed due

186 to the competition and N addition treatments (hypothesis 2), by using three-way ANOVAs on

187 invasive species responses. We used the same responses and factors in these ANOVAs as for

188 those on native species responses, although the factor "native species identity" now referred

189 to the identity of the native competitor.

190 If a three-way interaction occurred, then the analysis was split by native species identity/

191 native competitor identity in order to facilitate interpretation. In this case, two-way ANOVAs

192 were performed on the responses of each native species separately (or the invasive species in

193 competition with each native species separately) with competition treatment, N addition

194 treatment, and their interaction as factors. Tukey HSD pair-wise significant differences (p <

195 0.05) were determined between all levels of any significant factors, including any

196 interactions. Models that violated assumptions of normality or homoscedasticity received a

197 $\log_{10}(y)$ transformation. All analyses were performed in R version 3.2.4 (R Core Team 2016).

198

199 **Results**

200 BIOMASS RESPONSES

201 Native and invasive species growth was impacted in contrasting ways by the competition

202 treatments (Table 1; Fig. 2). Both native species responded similarly to competition with the

203 invader, expect for their belowground biomass (Fig. 2). Compared to the control treatment,

204 belowground competition with the invader reduced native species mean total biomass by a

205 third, whilst full competition reduced it by half (F = 24.6, $p < 0.01$, Table 1, Fig. 2a).

206 Conversely, belowground competition with native species increased invasive species mean

207 total biomass by 41% and full competition increased it by 65% (F = 66.0, $p < 0.01$, Table 1,

208 Fig. 2a). Belowground and full competition between the native and invasive species increased

209 the mean percentage of dead aboveground biomass on native species by a factor of 4 (F =

210 44.7, $p < 0.01$, Table 2, Fig. S1), while reducing it on invasive species to almost half (F =

211 14.4, $p < 0.01$, Table 2, Fig. S1). Nitrogen addition decreased belowground biomass of native

212 species from 0.47 ± 0.05 g (mean $\pm$ one SE) to 0.38 ± 0.04 g and invasive species from $2.20 \pm$

213 0.09 g to 1.75 ± 0.08 g. It also increased invader aboveground biomass from 3.14 ± 0.14 g to

214 3.83 ± 0.18 g. Nonetheless, it did not affect total biomass or dead aboveground biomass, and

215 its effects did not change under the different competition treatments (Tables 1 & 2).

216 Aboveground competition on its own had no effect on native or invasive species growth;

217 however, when combined with belowground competition (i.e. in the full competition

218 treatment) it resulted in a ca. 25% greater decline in native species total biomass, and a

219   greater increase in invasive species biomass, than belowground competition on its own (Fig.

220   2a). The increase in invasive species total biomass in the full competition treatment was

221   principally driven by increases in aboveground biomass (Fig. 2b), not belowground biomass

222   (Fig. 2c); whereas the decline in native species total biomass came predominantly from a

223   decrease in belowground biomass (Fig. 2d).

224   RESOURCE CAPTURE AND ALLOCATION RESPONSES

225   *Total N content*

226   Mean total N content (g) of native and invasive species responded in similar but slightly more

227   complex ways to competition than their biomass. The impact of invasive species competition

228   varied by native species identity (F = 2.8, $p < 0.05$, Table 2, Fig. S2) and by N addition (F =

229   3.5, $p = 0.02$, Table 2, Fig. 3b). *P. cita*'s mean total N content declined by c. 40 and 50 %

230   when competing belowground and fully with the invader (Fig. S2), whereas the mean total N-

231   content of *P. colensoi* decreased by c. 60 and 75 % (Fig. S2), respectively. The negative

232   effect of belowground competition on native species mean total N was almost twice as large

233   under the low N treatment (-63%) than the high N treatment (-34%; Fig. 3b). Similarly, the

234   full competition treatment resulted in a 76% decrease under low N conditions compared with

235   a 55% decrease under high N conditions (Fig. 3b). Invasive species mean total N content

236   increased by over 50% when the invader competed with native species belowground, and by

237   over 75% when they competed fully (F = 79.8, $p < 0.01$, Table 2, Fig 3a), regardless of native

238   species competitor identity and N addition. Aboveground competition had no effect on native

239   or invasive species resource capture on its own; however, when combined with belowground

240   competition (i.e. in the full competition treatment), it resulted in a ~25% greater increase in

241   invasive species mean total N content than just belowground competition on its own (Fig.

242   3a).

243   *Mean C: N ratio and allocation patterns*

244   There was a three-way interaction between native species identity, competition and N

245   addition treatments on mean C: N ratio of native species (F = 3.3, p = 0.03, Table 2). We

246   therefore split the analysis by native species identity and tested *P. cita* and *P. colensoi*

247   responses separately (Table 3; Figs. 3c-d). The patterns in their responses were relatively

248   similar (Figs. 3c-d). They both showed stable mean C: N ratios across all competition

249   treatments under the high N treatment (Figs. 3c-d). Under the low-N treatment, they both

250   showed increased mean C: N ratios (*P. cita,* +37%; *P. colensoi* +44%) when competing

251   belowground with the invader (Figs. 3c-d). The key difference between the native species

252   was in the control and aboveground competition treatments; where the mean C: N ratio of *P.*

253   *cita* decreased in the high N treatment, compared to the low N treatment, while *P. colensoi's*

254   mean C: N ratio showed no difference (Figs. 3c-d). The mean C: N ratio of the invasive

255   species, *A. capillaris*, was mostly stable in response to competition treatments, although it

256   was slightly higher in the aboveground than the belowground or full competition treatments

257   (F = 4.0, *p = 0.01*, Table 2; Fig 3e).

258   The allocation patterns of the invasive species showed no significant variation in response to

259   competition treatments (Table 4; Fig. 3f & S3). However, compared to the control treatment,

260   the native species showed a lower RMF in the full competition treatment (F = 4.7, *p = <0.01*,

261   Table 4; Fig 3f), and a higher RNF in the belowground competition treatment compared to

262   the aboveground competition treatment (F = 3.2, *p = 0.03*, Table 4; Fig S3).

263

264   **Discussion**

265   Contrary to our expectations that aboveground competition would be more important than

266   belowground competition under elevated N availability, belowground competition was in fact

267   central to the impact of the invasive grass species regardless of N availability. The

268   belowground competitive superiority of the invasive grass, *A. capillaris*, caused large

269   declines in native species biomass and total N content, along with alterations to tissue

270   nutrient stoichiometry and biomass allocation patterns. The invader's impact was greatest

271   under low N conditions but it also remained a superior competitor under high N conditions.

272   Considering the paucity of invader impact studies explicitly separating above and

273   belowground competition, along with a general perception of invasive plants as exploitative

274   species that are likely to be stronger aboveground competitors, we suggest that belowground

275   competition may be an under-appreciated mechanism for invasive plant impacts. This is

276   particularly true in high fertility ecosystems, such as those experiencing N enrichment due to

277   global change.

278   COMPETITIVE IMPACT

279   We used direct measures of competition including resource capture, alongside indirect

280   measures such as biomass, in order to determine whether competitive interactions

281   underpinned the differences in species growth (Trinder et al. 2013). Since resource capture

282   rates, i.e. total N content, mirrored the changes in species biomass across competition

283   treatments, it is likely that competitive interactions underpinned these changes. In the full

284   competition treatment, native species' growth and resource capture rates were heavily

285   reduced, while the invader's growth and resource capture increased substantially (Figs. 1 and

286   2). This supports our first hypothesis that competition between the invasive, *A. capillaris*, and

287   the native grass species, *P. cita* and *P. colensoi*, benefits the invasive species and decreases

288   native species growth and resource capture, compared with intraspecific competition.

289   Competition is therefore a clear pathway for the negative impacts of *A. capillaris* on two co-

290   occurring native grasses. The invader's competitive advantage suggests that fitness

291   differences between the invader and native species are likely contributing to *A. capillaris's*

292   invasive success in these systems (MacDougall et al. 2009). Whilst other invasive plants have

293   been shown to out-compete native species, this often depends on increased nutrient

294   availability (Daehler 2003; Besaw et al. 2011; Seabloom et al. 2015). In contrast, the invader

295   in our study, *A. capillaris*, had large impacts on native species across both high and low N

296   availabilities. This is consistent with previous experiments in native grassland communities,

297   which also found no significant change in competition intensity across soil nutrient gradients

298   (Wilson and Shay 1990; DiTommaso and Aarssen 1991), particularly when interspecific

299   competition intensity is calculated relative to intraspecific competition intensity (Grace 1993;

300   Turkington et al. 1993). For the invader in our study, *A. capillaris*, such universal superior

301   performance over co-occurring native species suggests that *A. capillaris* may be a rare

302   "super-invader" (Daehler 2003). This could partly explain its increasing dominance in native

303   New Zealand grasslands since the 1960s (Rose 1995; Rose et al. 2004).

304   ABOVE VS. BELOWGROUND COMPETITION

305   The invasive grass's superior competitive ability, along with its negative impact on native

306   plant species, was driven by better capture of belowground resources. Evidence for this

307   comes from the decreases in total N content and increases in C: N ratios of native species in

308   the belowground competition treatment relative to the control treatment, along with the co-

309   occurring increases in total N content of the invader. This clearly demonstrates that

310   belowground competition allowed the invader to capture key resources required for plant

311   growth, in this case soil nitrogen, which the native species would otherwise have acquired. It

312   is also possible that release from belowground intraspecific competition allowed the invader

313   to grow faster and larger. In contrast, when native species were released from belowground

314   intraspecific competition their biomass decreased (fig. 1). The only two other studies that

315   separated above and belowground competition explicitly between native and invasive species

316   also both reported that belowground competition was more important in mediating invader

317   impacts than aboveground competition (Dillenburg et al. 1993; Kueffer et al. 2007).

318   However, these experiments tested functionally dissimilar plant species, namely lianas and

319   trees (Dillenburg et al. 1993) or adult trees and saplings (Kueffer et al. 2007), which means

320   their results are influenced by differences in lifeform and stage (Vila and Weiner 2004). Our

321   results extend the findings of these previous studies by showing that belowground

322   competition is a key driver of invasive plant impacts within a single plant functional group,

323   life form and growth stage. In the broader literature, belowground competition has been

324   shown to play a crucial role in structuring plant communities (Fargione et al. 2003; Harpole

325   and Tilman 2006; Hillerislambers et al. 2012) and is often more important in determining

326   competitive outcomes than aboveground competition (Wilson 1988). Nevertheless, the two

327   types of competition are likely to interact (Cahill 2002), and in addition to the direct impact

328   of belowground competition in our study, there was also an indirect impact *via* the facilitation

329   of aboveground competitive interactions. There are three lines of evidence for this. Firstly,

330   the aboveground competition treatment had no effect on native or invasive species responses.

331   Secondly, the full competition treatment had a stronger effect on native and invasive species

332   total biomass responses than the belowground competition treatment. Thirdly, this greater

333   impact on native species biomass responses was accompanied by an increase in invader

334   aboveground biomass (Fig. 2b), suggesting the additional impact on native species is likely to

335   have been driven by shading effects. Nonetheless, the impact of aboveground competition in

336   the full competition treatment was still entirely reliant on the invader's superior capture of

337   belowground resources.

338   The invasive grass's capacity to out-compete the native grasses for belowground resources

339   may be related to its greater root biomass relative to the natives (Figs. 2c-d), since

340 belowground competition appears to be size-symmetric (Cahill and Casper 2000). Root

341 biomass, alongside other root traits, may be influential in driving invasive grass species

342 success (Thomsen et al. 2006), which potentially makes it a useful screening tool.

343 Nonetheless, root biomass alone is unlikely to determine belowground competitive outcomes

344 between species (Cahill 2003), but typically interacts with other factors, such as feedbacks

345 with soil biota (van der Putten et al. 2016). For example, belowground enemy release may

346 also have facilitated the invasive grass's superior competitive abilities belowground (Agrawal

347 et al. 2005; Reinhart and Callaway 2006). Likewise, allelopathic effects cannot be excluded;

348 although we found no evidence in the literature that *A. capillaris* has allelopathic effects on

349 co-occurring species. While the exact reason for *A. capillaris'* belowground superiority is

350 difficult to determine, our results clearly demonstrate that belowground competition is central

351 to delivering this invader's impact.

352 NITROGEN AVAILABILITY

353 While higher N-availability increased the aboveground biomass of the invasive grass but not

354 the native species, it did not increase the invader's impact on native species. Nor did it

355 diminish the relative importance of belowground competition. This contradicts our second

356 hypothesis that *A. capillaris'* competitive impacts on native species, and the relative

357 importance of aboveground competition over belowground competition, both increase with

358 increasing N availability. In fact, native species showed significantly greater reductions in

359 total N content, in response to belowground competition with the invader, under low N

360 conditions than high N conditions. Furthermore, it was only under low N conditions that

361 belowground competition with the invader altered native species tissue nutrient stoichiometry

362 (i.e. increased their C: N ratios). Nitrogen was therefore likely a limiting resource in our

363 experiment, as supported by various lines of evidence. Firstly, the exceptionally low N:P ratio

364 (0.6) of the soil was lower than the critical N:P ratio in aboveground vegetation (ca. 15);

365   below which growth is limited by N (Olde Venterink et al. 2003; Olde Venterink and

366   Güsewell 2010). Secondly, nitrogen addition, in the high N treatment, alleviated the negative

367   impact of belowground competition on native species N capture rates but not their biomass.

368   This suggests the invader out-competed the natives for other belowground resources in the

369   high N treatment, which are essential for growth and either became limiting following N

370   addition, or were co-limiting (Harpole et al. 2011). It is surprising that N addition did not

371   enhance invader impact as non-native grass invasions in New Zealand, and elsewhere, are

372   often associated with increased N availability (Dickie et al. 2014; Seabloom et al. 2015).

373   Furthermore, native grasses that are adapted to low fertility soils, such as those in our study,

374   may not respond to added nutrients, or in some cases may even respond negatively; unlike

375   exotic invasive grasses which often respond positively (Thompson and Leishman 2004;

376   Leishman and Thomson 2005; Radford et al. 2007; Seabloom et al. 2015). However, in its

377   native range, *A. capillaris* is not considered a high-N species (Hill et al. 1999) and invasive

378   plants can also succeed in low fertility environments (Funk and Vitousek 2007; Heberling

379   and Fridley 2016), despite some efforts to restore native species by soil fertility reduction

380   (e.g. Blumenthal et al. 2003). Invasive plants that out-compete co-occurring native species

381   across wide gradients of soil fertility, such as *A. capillaris* in New Zealand grasslands, are

382   likely to have the highest net impacts on native plant communities.

383   CONCLUSION

384   The invasive grass *A. capillaris* reduced co-occurring native grass species biomass by half,

385   and their resource capture by up to 75%. These impacts were driven directly and indirectly by

386   belowground, not aboveground, competition - regardless of N availability. The invader's

387   greater root biomass appeared to facilitate its belowground competitive advantage. However,

388   future studies could incorporate other root traits in order to improve our understanding of

389   native – invasive plant root interactions, as this is currently underdeveloped in comparison

390 with our knowledge of aboveground interactions. The overriding influence of belowground

391 competition across wide levels of N availability in our study was unexpected, as the relative

392 importance of aboveground competition often increases with increasing soil N availability

393 (Wilson and Tilman 1991). Nevertheless, recent analyses reveal the prevalence of nutrient co-

394 limitation across ecosystems globally, including grasslands (Harpole et al. 2011; Fay et al.

395 2015), which underlines the significance of belowground competition for multiple soil

396 nutrients (Harpole and Tilman 2007; Harpole et al. 2016). In light of these findings, our

397 results suggest that belowground competition may be under-appreciated as invasive plant

398 impact mechanism, particularly in high fertility ecosystems, such as those experiencing N

399 enrichment due to global change. Our findings could help to improve predictions of the

400 impact on native species diversity of two pervasive, and interacting, drivers of global

401 environmental change.

402

409

410 **References**

411 Aerts R (1999) Interspecific competition in natural plant communities: mechanisms, trade-

412   offs and plant–soil feedbacks. J Exp Bot 50:29–37. doi: 10.1093/jexbot/50.330.29

413   Agrawal A, Kotanen P, Mitchell C, et al (2005) Enemy release? An experiment with

414   congeneric plant pairs and diverse above-and belowground enemies. Ecology 86:2979–

415   2989.

416   Barney JN, Tekiela DR, Barrios-Garcia MN, et al (2015) Global Invader Impact Network

417   (GIIN): Toward standardized evaluation of the ecological impacts of invasive plants.

418   Ecol Evol 5:2878–2889. doi: 10.1002/ece3.1551

419   Barney JN, Tekiela DR, Dollete ESJ, Tomasek BJ (2013) What is the real impact of invasive

420   plant species? Front Ecol Environ 11:322–329. doi: 10.1890/120120

421   Besaw LM, Thelen GC, Sutherland S, et al (2011) Disturbance, resource pulses and invasion:

422   Short-term shifts in competitive effects, not growth responses, favour exotic annuals. J

423   Appl Ecol 48:998–1006. doi: 10.1111/j.1365-2664.2011.01988.x

424   Blumenthal DM, Jordan NR, Russelle MP (2003) Soil carbon addition controls weeds and

425   facilitates prairie restoration. Ecol Appl 13:605–615.

426   Bobbink R (1991) Effects of Nutrient Enrichment in Dutch Chalk Grassland. J Appl Ecol

427   28:28–41.

428   Borer ET, Seabloom EW, Gruner DS, et al (2014) Herbivores and nutrients control grassland

429   plant diversity via light limitation. Nature 508:517–20. doi: 10.1038/nature13144

430   Broadbent AAD, Orwin KH, Peltzer DA, et al (2017) Invasive N-fixer Impacts on Litter

431   Decomposition Driven by Changes to Soil Properties Not Litter Quality. Ecosystems

432   20:1–13. doi: 10.1007/s10021-016-0099-3

433   CABI (2017) Invasive Species Compendium. Wallingford, UK CAB Int. www.cabi.org/isc.

434   Cahill JF (2002) Interactions between root and shoot competition vary among species. Oikos

435   99:101–112. doi: 10.1034/j.1600-0706.2002.990111.x

436   Cahill JF (1999) Fertilization Effects on Interactions Between Above- and Belowground

437   Competition. Ecology 80:466–480.

438   Cahill JF (2003) Lack of relationship between below-ground competition and allocation to

439   roots in 10 grassland species. J Ecol 91:532–540.

440   Cahill JF, Casper BB (2000) Investigating the relationship between neighbor root biomass

441   and belowground competition: field evidence for symmetric competition belowground.

442   Oikos 90:311–320. doi: 10.1034/j.1600-0706.2000.900211.x

443   Craine JM, Lee WG (2003) Covariation in leaf and root traits for native and non-native

444   grasses along an altitudinal gradient in New Zealand. Oecologia 134:471–8.

445   Daehler C (2003) Performance comparisons of co-occurring native and alien invasive plants:

446   implications for conservation and restoration. Annu Rev Ecol Evol Syst 34:183–211.

447   Daly GT (1964) Leaf-surface Wax in Poa colensoi. J Exp Bot 15:160–165.

448   Dickie IA, St John MG, Yeates GW, et al (2014) Belowground legacies of Pinus contorta

449   invasion and removal result in multiple mechanisms of invasional meltdown. AoB

450   Plants 6:1–15. doi: 10.1093/aobpla/plu056

451   Dillenburg LR, Whigham DF, Teramura AH, Forseth IN (1993) Effects of below- and

452   aboveground competition from the vines Lonicera japonica and Parthenocissus

453   quinquefolia on the growth of the tree host Liquidambar styraciflua.Oecologia 93:48–54.

454   DiTommaso A, Aarssen LW (1991) Effect of nutrient level on competition intensity in the

455   field for three coexisting grass species. J Veg Sci 2:513–522. doi: 10.2307/3236033

456   Duncan RP, Webster RJ, Jensen CA (2001) Declining plant species richness in the tussock

457   grasslands of Canterbury and Otago , South Island , New Zealand. New Zealand Journal

458   Ecology 2:35–47.

459   Edgar E, Connor H (2000) Flora of New Zealand. Volume V. Manaaki Whenua Press

460   Edgar E, Forde MB (1991) Agrostis L. in New Zealand. New Zealand Journal Botany

461   29:139–161. doi: 10.1080/0028825X.1991.10416717

462   Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: An

463   experimental test of neutral versus niche processes. PNAS 100:8916–8920.

464   Fay PA, Prober SM, Harpole WS, et al (2015) Grassland productivity limited by multiple

465   nutrients. Nat Plants 1:15080. doi: 10.1038/nplants.2015.80

466   Firn J, Moore JL, MacDougall AS, et al (2011) Abundance of introduced species at home

467   predicts abundance away in herbaceous communities. Ecol Lett 14:274–81

468   Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource

469   systems. Nature 446:1079–81. doi: 10.1038/nature05719

470   Grace JB (1993) The effects of habitat productivity on competition intensity. Trends Ecol

471   Evol 8:229–230. doi: 10.1016/0169-5347(93)90194-T

472   Harpole WS, Ngai JT, Cleland EE, et al (2011) Nutrient co-limitation of primary producer

473   communities. Ecol Lett 14:852–862. doi: 10.1111/j.1461-0248.2011.01651.x

474   Harpole WS, Sullivan LL, Lind EM, et al (2016) Addition of multiple limiting resources

475   reduces grassland diversity. Nature 537:1–9. doi: 10.1038/nature19324

476   Harpole WS, Tilman D (2006) Non-neutral patterns of species abundance in grassland

477   communities. Ecol Lett 9:15–23. doi: 10.1111/j.1461-0248.2005.00836.x

478   Harpole WS, Tilman D (2007) Grassland species loss resulting from reduced niche

479   dimension. Nature 446:791–3. doi: 10.1038/nature05684

480   Hautier Y, Niklaus P a, Hector A (2009) Competition for light causes plant biodiversity loss

481   after eutrophication. Science 324:636–8. doi: 10.1126/science.1169640

482   Heberling JM, Fridley JD (2016) Invaders do not require high resource levels to maintain

483   physiological advantages in a temperate deciduous forest. Ecology 97:874–884. doi:

484   10.1890/15-1659.1

485   Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) Ellenberg's indicator values for British

486   plants. ECOFACT Volume 2 Technical Annex.

487   Hillerislambers J, Adler PB, Harpole WS, et al (2012) Rethinking Community Assembly

488   through the Lens of Coexistence Theory. Annu Rev Ecol Evol Syst 43:227–48.

489   Johnson NC, Rowland DL, Corkidi L, Allen EB (2008) PLANT WINNERS AND LOSERS

490   DURING GRASSLAND N-EUTROPHICATION DIFFER IN BIOMASS

491   ALLOCATION AND MYCORRHIZAS. Ecology 89:2868–2878.

492   Kueffer C, Schumacher E, Fleischmann K, et al (2007) Strong below-ground competition

493   shapes tree regeneration in invasive Cinnamomum verum forests. J Ecol 95:273–282.

494   Lai HR, Mayfield MM, Gay-des-combes JM, et al (2015) Distinct invasion strategies

495   operating within a natural annual plant system. Ecol Lett 18:336–346.

496   Leishman MR, Haslehurst T, Ares A, Baruch Z (2007) Leaf trait relationships of native and

497   invasive plants: Community- and global-scale comparisons. New Phytol 176:635–643.

498   Leishman MR, Thomson VP (2005) Experimental evidence for the effects of additional

499   water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury

500   Sandstone soils, Sydney, Australia. J Ecol 93:38–49.

501   Leishman MR, Thomson VP, Cooke J (2010) Native and exotic invasive plants have

502   fundamentally similar carbon capture strategies. J Ecol 98:28–42.

503   Levine JM, Vilà M, D'Antonio CM, et al (2003) Mechanisms underlying the impacts of

504   exotic plant invasions. Proc R Soc B Biol Sci 270:775–81. doi: 10.1098/rspb.2003.2327

505   MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. J Ecol 97:609–

506   615. doi: 10.1111/j.1365-2745.2009.01514.x

507   Mark AF, McLennan B (2005) The conservation status of New Zealand's indigenous

508   grasslands. New Zealand Journal Botany 43:245–270.

509   Olde Venterink H, Güsewell S (2010) Competitive interactions between two meadow grasses

510   under nitrogen and phosphorus limitation. Funct Ecol 24:877–886.

511   Olde Venterink H, Wassen MJ, Verkroost AWM, De Ruiter PC (2003) Species richness-

512   productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84:2191–

513   2199. doi: 10.1890/01-0639

514   Ordonez A, Olff H (2013) Do alien plant species profit more from high resource supply than

515   natives? A trait-based analysis. Glob Ecol Biogeogr 22:648–658.

516   Ordonez A, Wright IJ, Olff H (2010) Functional differences between native and alien species:

517   a global-scale comparison. Funct Ecol 24:1353–1361.

518   R Core Team (2016) R: A language and environment for statistical computing.

519   Radford IJ, Dickinson KJM, Lord JM (2007) Functional and performance comparisons of

520   invasive Hieracium lepidulum and co-occurring species in New Zealand. Austral Ecol

521   32:338–354. doi: 10.1111/j.1442-9993.2007.01700.x

522   Reinhart K, Callaway R (2006) Soil biota and invasive plants. New Phytol 445–457.

523   Rose A (1995) Vegetation change over 25 years in a New Zealand short-tussock grassland:

524   effects of sheep grazing and exotic invasions. New Zealand Journal of Ecology 19(2):

525   163-174

526   Rose AB, Frampton CM (2007) Rapid short-tussock grassland decline with and without

527   grazing, Marlborough, New Zealand. New Zealand Journal of Ecology 31:232–244.

528   Rose AB, Suisted PA, Frampton CM (2004) Recovery, invasion, and decline over 37 years in

529   a Marlborough short tussock grassland, New Zealand. New Zealand Journal of Botany

530   42:77–87. doi: 10.1080/0028825X.2004.9512891

531   Scott D (2000) Fertiliser and grazing rejuvenation of fescue tussock grassland. New Zealand

532   Journal Agricultural Research 43:481–490. doi: 10.1080/00288233.2000.9513444

533   Seabloom EW, Borer ET, Buckley YM, et al (2015) Plant species' origin predicts dominance

534   and response to nutrient enrichment and herbivores in global grasslands. Nat Commun

535   6:7710. doi: 10.1038/ncomms8710

536   Seabloom EW, Harpole WS, Reichman OJ, Tilman D (2003) Invasion, competitive

537   dominance, and resource use by exotic and native California grassland species. Proc

538   Natl Acad Sci U S A 100:13384–9. doi: 10.1073/pnas.1835728100

539   Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of nitrogen deposition on the

540   species richness of grasslands. Science 303:1876–9. doi: 10.1126/science.1094678

541   Thompson VP, Leishman MR (2004) Survival of native plants of Hawkesbury Sandstone

542   communities with additional nutrients: effect of plant age and habitat type. Aust J Bot

543   52:141–147.

544   Thomsen MA, Corbin JD, D'Antonio CM (2006) The effect of soil nitrogen on competition

545   between native and exotic perennial grasses from northern coastal California. Plant Ecol

546   186:23–35. doi: 10.1007/s11258-006-9109-4

547   Tilman D (1988) Plant strategies and the dynamics and structure of plant communities.

548   Princeton University Press, Princeton, New Jersey, USA.

549   Tilman D (1982) Resource Competition and Community Structure. Princeton University

550   Press. Princeton, USA.

551   Trinder CJ, Brooker RW, Robinson D (2013) Plant ecology's guilty little secret:

552   Understanding the dynamics of plant competition. Funct Ecol 27:918–929.

553   Turkington R, Klein E, Chanway CP (1993) Interactive effects of nutrients and disturbance:

554   an experimental test of plant strategy theory. Ecology 74:863–878.

555   Tylianakis JM, Didham RK, Bascompte J, Wardle D a. (2008) Global change and species

556   interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363.

557   van der Putten WH, Bradford MA, Pernilla Brinkman E, et al (2016) Where, when and how

558   plant-soil feedback matters in a changing world. Funct Ecol 1109–1121.

559   Van Kleunen M, Dawson W, Essl F, et al (2015) Global exchange and accumulation of non-

560   native plants. Nature 525:100–103. doi: 10.1038/nature14910

561   van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between

562   invasive and non-invasive plant species. Ecol Lett 13:235–45.

563   Vilà M, Espinar JL, Hejda M, et al (2011) Ecological impacts of invasive alien plants: a

564   meta-analysis of their effects on species, communities and ecosystems. Ecol Lett

565   14:702–8. doi: 10.1111/j.1461-0248.2011.01628.x

566   Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant

567   species?–evidence from pair-wise experiments. Oikos 105: 229-238

568   Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's

569   Ecosystems. Science 277:494–499. doi: 10.1126/science.277.5325.494

570   Williams PA (1998) Response of broom (Cytisus scoparius) to control measures. Sci Conserv

571   report, Dep Conserv New Zeal 97.

572   Wilsey BJ, Polley WH (2006) Aboveground productivity and root-shoot allocation differ

573   between native and introduced grass species. Oecologia 150:300–309.

574   Wilson JB (1988) SHOOT COMPETITION AND ROOT COMPETITION. J Appl Ecol

575   25:279–296.

576   Wilson SD, Shay JM (1990) Competition, Fire, and Nutients in a Mixed-Grass Prairie.

577   Ecology 71:1959–1967. doi: 10.2307/1937604

578   Wilson SD, Tilman D (1991) Component of Plant Competition Along an Experimental

579   Gradient of Nitrogen Availability. Ecology 72:1050–1065. doi: 10.2307/1940605

580

581

582

583

584

585

586

587 **Tables**

588 **Table 1** Results of 3-way ANOVAs testing effects of native species identity (NSI),

589 competition (C), nitrogen addition (N+) and their interactions on biomass responses (total,

590 aboveground and belowground) of native (*Poa cita* and *Poa colensoi*) and invasive species

591 (*Agrostis capillaris*). All factors are fixed effects. Biomass data were log-transformed before

592 analysis.

		Total biomass		Aboveground biomass		Belowground biomass	
	df	*F*	*P*	*F*	*P*	*F*	*P*
Native species							
NSI	1	222.5	<0.01	221.1	<0.01	178.2	<0.01
C	3	24.6	<0.01	18.7	<0.01	30.8	<0.01
N+	1	0.5	0.48	0.4	0.54	10.8	<0.01
NSI * C	3	0.8	0.51	0.9	0.47	4.3	<0.01
NSI * N+	1	1.0	0.31	1.2	0.28	1.6	0.21
C * N+	3	0.3	0.80	0.6	0.61	0.6	0.60
NSI * C * N+	3	0.8	0.51	0.7	0.57	1.5	0.21
Invasive species							
NSI	1	2.1	0.15	4.9	0.03	0.03	0.86
C	3	66.0	<0.01	49.1	<0.01	23.0	<0.01
N+	1	1.9	0.18	30.1	<0.01	26.3	<0.01
NSI * C	3	1.4	0.25	1.3	0.28	0.7	0.53
NSI * N+	1	0.7	0.42	0.1	0.82	0.8	0.37
C * N+	3	1.3	0.28	2.3	0.09	0.2	0.93
NSI * C * N+	3	1.3	0.29	0.4	0.77	1.5	0.22

593

594 **Table 2** Results of 3-way ANOVAs testing effects of native species identity (NSI),

595 competition (C), nitrogen addition (N+) and their interactions on % dead aboveground (AG)

596 biomass, total N content and C/N ratio of native (*P. cita* and *P. colensoi*) and invasive species

597 (*A. capillaris*). All factors are fixed effects. Total N content and CN ratio data were log-

598 transformed before analysis.

	df	% Dead AG biomass		Total N content		C/N ratio	
	df	*F*	*P*	*F*	*P*	*F*	*P*
Native species							
NSI	1	1.7	0.20	154.0	<0.01	0.2	0.68
C	3	44.7	<0.01	56.6	<0.01	4.5	<0.01
N+	1	0.1	0.74	65.9	<0.01	206.2	<0.01
NSI * C	3	0.2	0.87	2.8	0.05	1.7	0.18
NSI * N+	1	0.4	0.54	13.5	<0.01	28.7	<0.01
C * N+	3	1.4	0.25	3.5	0.02	14.8	<0.01
NSI * C * N+	3	0.7	0.57	1.1	0.36	3.3	0.03
Invasive species							
NSI	1	0.2	0.63	1.7	0.20	<0.1	0.87
C	3	14.4	<0.01	79.8	<0.01	4.0	0.01
N+	1	0.6	0.43	668.2	<0.01	1233.0	<0.01
NSI * C	3	1.1	0.35	0.7	0.53	0.9	0.42
NSI * N+	1	2.3	0.13	0.03	0.86	0.5	0.49
C * N+	3	0.3	0.82	1.1	0.36	1.3	0.27
NSI * C * N+	3	2.6	0.06	1.1	0.35	1.3	0.29

599

600 **Table 3** Results of 2-way ANOVAs testing effects of competition (C), nitrogen addition

601 (N+) and their interaction on CN ratio of native species (*P. cita* and *P. colensoi*). All factors

602 are fixed effects. *P. cita* data were log-transformed before analysis.

	CN ratio		
	df	*F*	*P*
P. cita			
C	3	4.1	0.01
N+	1	218.2	<0.01
C * N+	3	3.1	0.04
P. colensoi			
C	3	4.1	0.01
N+	1	37.0	<0.01
C * N+	3	13.7	<0.01

603

604

605

606

607

608

609

610

611

612

613 **Table 4** Results of 3-way ANOVAs testing effects of native species identity (NSI),

614 competition (C), nitrogen addition (N+) and their interactions on root mass fraction (RMF)

615 and root nitrogen fraction (RNF) of native (*P. cita* and *P. colensoi*) and invasive species (*A.*

616 *capillaris*). All factors are fixed effects. Invasive species data were log-transformed before

617 analysis.

		RMF		RNF	
	df	*F*	*P*	*F*	*P*
Native species					
NSI	1	<0.1	0.82	5.9	0.02
C	3	4.7	<0.01	3.2	0.03
N+	1	20.5	<0.01	22.7	<0.01
NSI * C	3	0.3	0.84	2.4	0.07
NSI * N+	1	0.1	0.82	0.3	0.58
C * N+	3	0.7	0.57	0.4	0.77
NSI * C * N+	3	1.8	0.16	0.9	0.44
Invasive species					
NSI	1	2.4	0.12	0.2	0.69
C	3	0.7	0.53	1.9	0.14
N+	1	69.2	<0.01	74.6	<0.01
NSI * C	3	0.7	0.56	0.2	0.87
NSI * N+	1	0.3	0.61	0.5	0.50
C * N+	3	1.3	0.30	0.7	0.56
NSI * C * N+	3	0.5	0.66	1.3	0.28

618

619

620

Figure legends

Fig. 1 Schematic diagram showing experimental setup for invasive (I) and native (N) species

planted in pots with above and belowground partitions to create four competition treatments:

a) Control - full intraspecific competition between a pair of invasive and a pair native

individuals, but no interspecific competition; b) Aboveground - aboveground interspecific

competition between invasive and native individuals, and belowground intraspecific

competition; c) Belowground - belowground interspecific competition between invasive and

native individuals and aboveground intraspecific competition and d) Full - above and

belowground interspecific competition between invasive and native individuals but no

intraspecific competition. In a) and d) the above and belowground partitions were flush; they

are depicted lightly apart for clarity.

Fig. 2 Biomass responses of native and invasive species to four competition treatments (See

Fig. 1 legend for full description). a) Total biomass; b) aboveground biomass for native and

invasive species; c) below-ground biomass for invasive species; d) below-ground responses

of two native species, *P. cita* and *P. colensoi* to these treatments. Box-and-whisker plots

show individual data points, means, one standard error and range of data. Means with the

same letter are not significantly different ($p > 0.05$, Tukey HSD post hoc tests); in a) and b)

upper case letters are for ANOVAs comparing invader responses; lower case for native

species responses

Fig. 3 Resource capture and allocation responses of native and invasive species to four

competition treatments (See Fig. 1 legend for full description). a) Total N content for invasive

species; b) total N content for native species in high or low N treatments; c) C/N ratio for *P.*

cita in different N treatments; d) C/N ratio for *P. colensoi* in different N treatments; e) C/N

ratio for invasive species; f) root mass fraction (RMF) for native and invasive species. Box-

645   and-whisker plots show individual data points, means, one standard error and range of data.

646   Means with the same letter are not significantly different (p > 0.05, Tukey HSD post hoc

647   tests); in f) upper case letters are for ANOVAs comparing invader responses; lower case for

648   native species responses

Fig. 1

Fig. 2

Fig.3