1    **Invasion by *Fallopia japonica* increases topsoil mineral nutrient**

2    **concentrations**

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15

16 **Abstract**

17

18 *Fallopia japonica* is one of the most troublesome alien invasive plants across temperate

19 regions, with large negative impacts on plant species diversity. We examined its impacts

20 on topsoil chemistry and nutrient stocks in standing biomass at six sites with contrasting

21 resident plant community in Belgium. Topsoil and biomass were sampled in invaded and

22 closely adjacent uninvaded plots. Standing biomass and mineral nutrient concentrations in

23 soil (ammonium acetate exchangeable cations and P, total C and N) and plants were

24 determined. Soil under *F. japonica* generally had higher exchangeable nutrient

25 concentrations (Cu: +45%, K: +34%, Mg: +49%, Mn: +61%, P: +44%, Zn: +75%).

26 Standing biomass was 3- to 13-fold higher depending on site. Despite lower nutrient

27 concentrations in aboveground biomass, invaded stands had 3.2- to 5.4-fold larger nutrient

28 stocks in abovegroud biomass compared to the resident vegetation. We conclude that *F.*

29 *japonica* enhances nutrient cycling rates and topsoil fertility, probably due to nutrient

30 uplift. The impacts were most large in sites with low nutrient concentrations in uninvaded

31 plots, suggesting that *F. japonica* may contribute to soil homogenization in invaded

32 landscapes.

33

34 **Résumé**

35

36 *Fallopia japonica* est une des espèces de plante exotique envahissante les plus

37 problématique à l'échelle mondiale avec un impact négatif important sur la diversité

38 végétale. Nous avons examiné ses impacts sur la chimie du sol superficiel et sur les stocks

39 de nutriments dans la biomasse sur pied dans six sites à végétations contrastées. Le sol et la

40 biomasse ont été échantillonnés dans des placeaux envahis et non-envahis adjacents. La

41 biomasse sur pied et la concentration en éléments minéraux dans le sol (cations et P

42 échangeables à l'acétate d'ammonium, C et N total) et dans les plantes ont été déterminées.

43 Le sol sous *F. japonica* présentait généralement des concentrations en nutriments

44 échangeables plus élevées (Cu: +45%, K: +34%, Mg: +49%, Mn: +61%, P: +44%, Zn:

45 +75%). La biomasse sur pied était de 3 à 13 fois plus élevée selon le site. Malgré les

46 concentrations en nutriments plus faible dans la biomasse aérienne, les placeaux envahis

47 avaient des stocks de nutriments dans la biomasse aérienne de 3.2 à 5.4 fois plus

48 importants que la végétation indigène. Nous concluons que *F. japonica* augmente les flux

49 de nutriments dans l'écosystème et la fertilité du sol superficiel, probablement en raison

50 d'une remontée de nutriments en provenance d'horizons plus profonds. Les impacts étaient

51 les plus grands dans les sites à faibles concentrations de nutriments dans les placeaux non

52 envahis, ce qui suggère que *F. japonica* pourrait contribuer à l'homogénisation des sols

53 dans les paysages envahis.

54

55 **Key words:** Alien invasive species, exotic species, *Fallopia japonica*, homogenization,

56 nutrient cycling, nutrient uplift.

57

58 **Nomenclature: Plants:** Lambinon et al., 2004

59       **Phytosociological syntaxons** : Bournérias et al., 2001

60  **Introduction**

61

62  Biological invasions are now considered as one of the major causes of biodiversity loss

63  worldwide (D'Antonio & Meyerson, 2002). Exotic plant invasions often have dramatic

64  impacts on the resident vegetation by modifying its composition and structure (Levine *et*

65  *al.*, 2003). Most of the time, the driving force of this direct impact is competition for

66  resources (light, water, nutrients). The more subtle impacts of plant invasions on

67  ecosystem functioning are comparatively less studied. Two important factors controlling

68  ecosystem functioning are soil properties and nutrient fluxes between plant and soil. The

69  review of Ehrenfeld (2003) concluded that invasive species most often increased

70  productivity of invaded ecosystems and enhanced N availability by the restitution of a

71  more easily decomposable litter compared to the resident vegetation. Compared to C and

72  N, the impacts of invasions on base cations and phosphorus availability have been rarely

73  assessed. From the scarce data available, it appears that increased nutrient availability has

74  been more often observed than decreased availability (Musil, 1993; Scott *et al.*, 2001;

75  Vanderhoeven *et al.*, 2005; Chapuis-Lardy *et al.*, in press but see Belnap & Philips, 2001).

76  However, most of these studies consider the impacts of one species at one particular site.

77  Their results are thus difficult to generalize since one species can have contrasting impacts

78  depending on site (Belnap & Philips, 2001; Scott *et al.*, 2001).

79      In Belgium, many alien invasive plant species have dramatically increased their range

80  during the last decades. One of these is Japanese Knotweed (*Fallopia japonica* (Houtt.)

81  Ronse Decraene)*,* one of the most successful and troublesome exotic species in Europe and

82  elsewhere (Pysek *et al.*, 2001, Verloove, 2002; Saintenoy-Simon, 2003; Weber, 2003;

83  Muller, 2004). By the way, it has been included in the list of the "100 of the World's Worst

84  Invasive Alien Species" (ISSG). Originating from East Asia, it was introduced in Belgium

85  at the end of the 19th century and is now found in all regions of the country (Verloove,

86  2002; Saintenoy-Simon, 2003). *F. japonica* is a shrub-like rhizomatous geophyte and thus

87  belongs to a functional type not represented in the native vegetation. In Europe, the

88  reproduction of *Fallopia japonica* is only vegetative. Hollingsworth and Bailey (2000)

89  demonstrated that all individuals of *Fallopia japonica* in UK (150 samples + 16 samples

90  across Europe and the USA) have the same genotype and must thus be considered as a

91  large widespread clone. Fragments of rhizomes and stems easily resprout and can be

92  carried by streams or animals (Weber 2003). The main dispersion agent is human activity

93  through the movement of topsoil containing plant fragments (Child *et al.*, 2001).

94  Being a geophyte, *F. japonica* leaves the soil bare during winter, which is very

95  different from the indigenous vegetation. It has aerial annual stems up to 3 meter high and

96  is able to form very dense monospecific patches (Beerling *et al.*, 1994). Its rhizome system

97  is very dense and can grow to 2 meter in depth (Child *et al.*, 2001). *F. japonica* often

98  achieves competitive exclusion of native plant species mainly due to competition for light

99  (Hathaway, 1999; Verloove, 2002). In forest, dense clones may also block tree

100  regeneration (Muller, 2004). *F. japonica* has also been shown to affect negatively native

101  animal communities. It notably reduces the diversity of phytophageous insects (Beerling &

102  Dawah, 1993) and reduces the foraging success of frogs in invaded areas (Maertz *et al.*,

103  2005). It is mainly found in wasteland, on road and railway banks, on river banks, in open

104  forests and other habitats strongly influenced by man (Beerling *et al.*, 1994). It tolerates a

105  wide range of soil conditions, from poor acidic soils to rich and/or calcareous soils

106  (Beerling *et al.*, 1994).

107  The management of this species is very difficult and most of the time not successful

108  (Muller, 2004). The monitoring of habitats not yet invaded and the limitation of soil

109  displacement are certainly the best way to prevent further expansion of the plant. In U.K.,

110    the use of soil "contaminated" with *F. japonica* for construction is prohibited; such soils

111    have to be carried in licensed landfill sites (Child *et al.*, 2001).

112        *F. japonica* has been extensively studied. Published studies concern its past and

113    present distribution (e.g.: Pysek *et al.*, 2001; Mandák *et al.*, 2004), possible impact of

114    climate change on its future distribution (Beerling *et al.*, 1995), genetic diversity

115    (Hollingsworth *et al.*, 1998; Hollingsworth & Bailey, 2000), impacts on native plant and

116    animal communities (Beerling & Dawah, 1993; Beerling *et al.*, 1994; Maertz *et al.*, 2005)

117    and management (Child & Wade, 2000; Child *et al.*, 2001; Bimova *et al.*, 2001).

118    Surprisingly, its impacts on soil properties and ecosystem processes in the introduced

119    range do not seem to have been investigated. For instance, the species is not cited in the

120    review of Ehrenfeld (2003). In its native range, *F. japonica* has been shown to influence

121    soil nitrogen patterns (Hirose & Tateno, 1984). During primary succession on volcanic

122    soils, organic and mineral forms of nitrogen accumulate under *Fallopia*. $N-NO_3^-$ has its

123    highest concentration under *Fallopia* and then decreases under the following species of the

124    succession. *F. japonica* has also been shown to reach a high relative growth rate even

125    under nitrogen-limited conditions (Chiba & Hirose, 1993).

126        In this paper, we examine the impacts of *Fallopia japonica* on soil chemical

127    properties, aboveground primary productivity and cycling of 8 nutrients by comparing

128    invaded and adjacent uninvaded plots as proposed by Walker and Smith (1996). Given that

129    alien invasive species can have different impacts depending on site (Scott *et al.*, 2001;

130    Ehrenfeld, 2003), six sites with contrasting resident vegetation have been sampled. Impacts

131    are generally higher when the invader belongs to a functional type not represented in the

132    native vegetation (Gill & Burke, 1999; Ehrenfeld, 2003), which is indeed the case of

133    *Fallopia japonica*.

134　**Materials and methods**

135

136　Site selection

137

138　Six sites were selected in ecosystems with contrasting resident vegetation structure and

139　composition, representing the range of habitats colonized by *Fallopia japonica* in Belgium.

140　The sites fulfilled the following conditions: 1) having well-established, and still expanding

141　clones of *Fallopia* surrounded by native uninvaded vegetation, 2) having sufficiently

142　homogeneous soil. Site selection tried to minimize the probability of differences occurring

143　before the invasion event. To that end, invaded and control uninvaded plots selected in

144　each site were in the same topographic situation and had the same soil texture. We verified

145　that soil texture was the same between invaded and control plots by determining coarse

146　(100 µm-2 mm) and fine (50-100 µm) sand content of all soil samples (water-sieving after

147　calcination and clay dispersion by Na-citrate 40 mg l$^{-1}$). A site was selected only if there

148　was no significant difference between invaded and control plots for these two parameters

149　and for the fine/coarse ratio (*t*-test). Moreover, the uninvaded control plots were located as

150　close as possible to the front of expansion of the invader. We can therefore assume that

151　differences observed between invaded and uninvaded soils are most likely due to

152　difference of vegetation and were not present before invasion occurred. Geographic

153　coordinates and names of sites are given in table I. The site "VK" is located in the "Forêt

154　de Soignes", a large beech forest in the south of Brussels established on loamy brown soil;

155　*F. japonica* has certainly been introduced there due to soil disturbance by forest logging.

156　The site "EN" is located in the same forest, close to a pond in a small valley formerly

157　planted with hybrid poplars and now recolonized by willows (*Salix cinerea*). The soil is a

158　gley soil with anmoor humus. Disturbance by logging activities may have facilitated

159    establishment of *F. japonica* in this site as well. The site "HAR" is a rough mesic grassland

160    established on abandoned cultivated field on loamy soil. *F. japonica* has certainly been

161    introduced there with garden waste deposits. The site "GBX" is a cultivated field margin

162    on loamy soil. *F. japonica* has probably been introduced by agricultural machines. The site

163    "FOR" was a rubbish dump and has been recovered by a layer of loamy soil contaminated

164    with *F. japonica* rhizomes. The site "GHI" is a rough grassland established on a slag heap

165    composed of stony (chalk)-loamy soil. *F. japonica* has been introduced with contaminated

166    soil.

167
168    Soil sampling

169

170    At each site, six 1-m² plots were located in invaded patches and six 1-m² plots were located

171    in adjacent, uninvaded vegetation. Phytosociological relevés were conducted in invaded

172    and uninvaded plots using the conventional abundance-dominance scale of Braun-Blanquet

173    (1972).

174        Soil was sampled from February to April. In each plot, five soil cores (0-10 cm depth,

175    litter discarded) were collected with a soil borer (4 cm in diameter, one core at each corner

176    of the square and one core at the centre of the square). These five cores were mixed up into

177    a single bulk sample for each plot. Soil samples were air-dried until constant weight and

178    sieved (< 2 mm).

179

180    Soil analysis

181

182    The following parameters were assessed on each sample. Soil pH was measured with a

183    glass electrode (stiff paste soil + 1M KCl). For acidic soils only, exchangeable protons and

184    aluminum were extracted with 1M KCl (10 g soil in 50 ml solution) and determined by

185    derivative titration curve. Ca, Mg, K, Cu, Zn, Mn and P were extracted with 1M

186    $CH_3COONH_4$ pH 4.65 (10 g soil in 50 ml solution) and determined by ICP-AES. Ca was

187    not determined for samples containing free $CaCO_3$. Cation exchange capacity (CEC =

188    $[Ca^{2+}]$ + $[K^+]$+ $[Mg^{2+}]$ + $[H^+]$ + $[Al^{3+}]$) and base saturation rate (Bs) were thereafter

189    computed (Bs = ($[Ca^{2+}]$ + $[K^+]$+ $[Mg^{2+}]$)/CEC) except for carbonated soils. C and N

190    content were assessed using a dry combustion C/N analyzer (NC-2100, Carlo Erba

191    Instruments, Italy). $CaCO_3$ content was assessed (dry combustion, Ströhlein dosimeter)

192    after calcination of organic matter at 450°C. Organic C content (Corg) was calculated as

193    the difference of total C and carbonate C.

194

## Biomass sampling and analysis

Aboveground biomass was harvested in August at the peak of biomass on the same plots as for soil sampling. The plant samples were dried at 70°C to constant weight. All material was first ground in a garden shredder (Viking, GE220). Then a subsample was more finely (0.12 mm) ground in a mill (Retsch, ZM100). This subsample was calcinated at 550°C during 8 h and ashes were dissolved in 0.5 M HCl. Ca, Mg, K, P, Mn, Pb, Zn and Cu were determined by ICP-AES (Varian Vista MPX). C and N content were assessed using a dry combustion C/N analyzer (NC-2100, Carlo Erba Instruments, Italy). The aboveground nutrient stock (mg m$^{-2}$) was then calculated as the product of mineral nutrient concentration and biomass. Biomass could not be collected in the site "VK" due to complete destruction of the invaded plots by managers of the forest.

## Statistical analyses

At each site, mean values of all parameters were compared between invaded and uninvaded plots by means of t-tests. Bonferroni correction was applied to t-tests based on the number of simultaneous tests for each variable (N = 6 sites). Secondly, for essential nutrients in the soil only (Ca, Mg, K, Mn, Zn, Cu, P), a chi-square test was used to compare the proportion of cases showing increased vs. decreased concentrations of exchangeable mineral nutrients with the expected proportion (50%-50%) under the null hypothesis that *F. japonica* has no systematic impact. This test was performed for all sites pooled. A two-way ANOVA was performed on all sites pooled, with 'site' (fixed) and 'invasion' (fixed) as main effects and 'site x invasion' as interaction effect. In this analysis, a significant site x invasion interaction indicates that impacts vary depending on site.

220    Logarithmic transformation was applied prior to ANOVA when necessary (soil: Cu, Mg,

221    P, Zn, C/N; aboveground nutrient stocks: C, N; plant C/N). Statistical analyses were

222    performed with Statistica 7.1 software (StatSoft Inc. 2005).

223

224 **Results**

225

226 Vegetation

227

228 The number of species in invaded plots ranged from 1 to 6 and was lower compared to

229 control plots (4-24) in five of the six sites and equal in only one site (table II). In three

230 sites, invaded plots consisted of monospecific *F. japonica* stands. Species composition of

231 resident vegetation was widely different according to site (table II), in line with the broad

232 niche range of *F. japonica* in Belgium. The site "EN" comprised characteristic species of

233 the *Alnion incanae* alliance (*Carex pendula, Chrysosplenium alternifolium, C.*

234 *oppositifolium*) with *Petasites hybridus* as dominant species. The site "HAR" is an

235 impoverished form of *Arrhenatherion elatioris* (*Arrhenatherum elatius, Heracleum*

236 *sphondylium*) progressively colonized by species of the *Artemisietea vulgaris* (*Tanacetum*

237 *vulgare, Cirsium arvense*). In site "GHI", vegetation is composed of species of the

238 *Arrhenatherion elatioris* alliance (*A. elatius, Senecio jacobea, Achillea millefolium,*

239 *Hypericum perforatum…*) and of species indicating humid soil (*Carex hirta, Eupathorium*

240 *cannabinum, Symphytum officinale*). The site VK comprises forest species of the *Fagion*

241 *sylvaticae* (*Athyrium filix-femina, Dryopteris dilatata*) with some indicators of

242 waterlogging due to soil compaction (*Juncus effusus, Deschampsia cespitosa, Polygonum*

243 *hydropiper*). In the sites "GBX" and "FOR", vegetation consists of nitrophilous wasteland

244 species (*Urtica dioica, Rubus sp., Galium aparine*). *U. dioica* and *Rubus* are also present in

245 all other sites. Both species are ruderalisation indicators which very often co-occur with *F.*

246 *japonica* throughout Europe (Beerling et al., 1994).

247

248    Soil

249

250    In line with the broad range of invaded ecosystems, *F. japonica* was found in very

251    different soil conditions ("Site" effect was highly significant for all soil parameters, Figure

252    1). Invaded sites ranged from oligotrophic and acidic soil (site VK: pH = 3.2, K = 63 mg

253    kg$^{-1}$, Mg = 37 mg kg$^{-1}$, P = 3.1 mg kg$^{-1}$) to calcareous soil (site "GHI": pH = 6.7) or

254    eutrophic soil (site "FOR": pH = 6.6, K = 260 mg kg$^{-1}$, Mg = 232 mg kg$^{-1}$, P = 103 mg kg$^{-}$

255    $^{1}$).

256        t-tests revealed significant differences in all sites (14 significant differences on 72

257    tests, Figure 1). pH was generally lower in invaded soils but not significantly. For major

258    nutrients (K, Mg, P) we found respectively one, two and one significant increased

259    availability in invaded soils but one significant decrease for K and P in the site "FOR". Mn

260    availability was always higher in invaded plots and the difference was significant for two

261    of the six sites. CEC was significantly higher in invaded plots in only 1 site (VK). For Ca,

262    H$^{+}$, Al$^{3+}$ and Bs, there was no significant difference between invaded and uninvaded plots

263    in any site. Increased availability of nutrients in invaded plots was significantly more

264    frequent than decreased availability (30 increases for 38 comparisons, $\chi^2$ = 12.74, *P* <

265    0.001). Concerning organic matter status, significant differences appear in three sites (For,

266    Ghi, Gbx). In the first two sites, C and N content was lower in invaded plots with

267    unchanged C/N ratio. In the third site, C and N content and C/N ratio increased in invaded

268    plots.

269        Differences between invaded (I) and uninvaded (U) plots can be expressed as the ratio

270    I/U (1 is the expected value of I/U under the null hypothesis that invasion has no impact).

271    The average value of I/U was calculated for all sites pooled (Figure 2). Figure 2 shows that

272    when all the sites are pooled, some general trends appear. In particular, there was a slight

273 decrease of pH in invaded plots (I/U ratio < 1) and a general increase in cations and P

274 availability (Cu: +45%, K: +34%, Mg: +49%, Mn: +61%, P: +44%, Zn: +75%). N, C and

275 C/N had I/U close to unity.

276     The results of two-way ANOVAs with site and invasion as main effects are presented

277 in Figure 1. There was a significant invasion effect for pH, Cu, Mg, Mn and Zn. The site

278 effect was significant for all parameters. The site x invasion interaction was significant for

279 Cu, K, Mg, P, Zn, C, N and C/N, indicating that impacts of invasion for these parameters

280 varied in direction and/or amplitude depending on local conditions. For instance, K, P and

281 Mg concentrations were significantly higher in invaded plots in site "GHI" but were lower

282 in site "FOR". The site "FOR" responded very differently to invasion by *F. japonica,* with

283 decreased values of K, Mg and P.

284

285 Biomass

286

287 Aboveground biomass of control vegetation ranged from 0.32 kg m$^{-2}$ in "Ghi" to 0.84 kg

288 m$^{-2}$ in "For" while the biomass of invaded plots ranged from 1.6 kg m$^{-2}$ in "EN" to 4.1 kg

289 m$^{-2}$ in "GHI". Values observed in invaded plots are 3 to 13 times higher than in uninvaded

290 native vegetation. This higher biomass of the invader was significant in all sites The two-

291 way ANOVA showed a significant invasion effect ($F = 150.8$ $P < 0.001$). The site and site

292 x invasion effects were also significant (Site: $F = 5.56$, $p<0.001$; Site x invasion: $F = 5.62$,

293 $p<0.001$).

294

295 Nutrient concentrations and stocks in plants

296

297　Mineral nutrient concentrations in abovegroud biomass were most often lower in invaded

298　compared to uninvaded plots, and this was significant 24 times for 45 tests (Table III). The

299　difference between invaded (I) and uninvaded (U) can be expressed as I/U ratio (Figure 3).

300　On average over all sites, I/U ratios ranged from 0.50 (P) to 0.79 (Mn). The difference was

301　largest for P (invaded: 644 - 2477 mg kg$^{-1}$, uninvaded: 1283 - 4913 mg kg$^{-1}$). The invasion

302　and site x invasion effect were highly significant for all elements (except Mn: no

303　significant site x invasion effect) (Table IV). In contrast to the other elements, C

304　concentrations and C/N ratio were systematically higher in invaded plots.

305　　　Due to much higher biomass, nutrient stocks were consistently higher in invaded

306　compared to uninvaded plots, with only few exceptions (30 significant increases on 45

307　tests) (Table III). The difference between invaded (I) and uninvaded (U) can be expressed

308　as I/U ratio (Figure 3). On average over all sites, I/U ratios ranged from 3.2 (P) to 5.4 (K).

309　The invasion and site x invasion effect were highly significant for all elements (except Ca

310　and K: no significant site x invasion effect) (Table IV). The site "For" standed out as a

311　striking exception, with similar values of nutrient stocks in biomass of invaded and control

312　plots; this site is the only one for which P stock was larger in the resident vegetation

313　(though the difference was not significant).

314

315　**Discussion**

316

317　Increased nutrients in topsoil

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319　A striking result is the finding of systematic differences between soil composition of

320　invaded and uninvaded, adjacent plots within all sites. There are two mutually non

321　exclusive explanations to these differences, i.e. pre-existing variation and plant-driven

322     variation in soil conditions. The first explanation requires that pre-existing variation in soil

323     conditions is governing the fine-scale distribution *of F. japonica* within all sites. Although

324     this mechanism cannot be formally ruled out, we believe it is highly unlikely, for the

325     following reasons. First, our sampling protocol was designed to reduce the possibility of

326     pre-existing differences in soil conditions between plots. Thus, homogeneity of soil texture

327     and soil profile were checked in all sites. *F. japonica* is still expanding in most selected

328     sites, and uninvaded plots were located close to the front of expansion of invaded stands.

329     Secondly, within site variation in soil condition is always much narrower than the range of

330     soil conditions encompassed by *F. japonica* across sites. It thus seems unlikely that fine-

331     scale variation in soil within sites is constraining expansion of *F. japonica*. In a formal

332     sense, impacts of plants on soil conditions can be formally proven only if time variation in

333     soil conditions following invasion is demonstrated. However, most published studies

334     demonstrating impacts of plant invasions have been performed at a single sampling date

335     (Asner & Beatty, 1996; Ehrenfeld *et al.*, 2001; Blank & Young, 2002; Duda *et al.*, 2003;

336     Standish *et al.*, 2004).

337       Despite site-specific effects, which will be discussed below, a general pattern of

338     increased availability of nutrients in topsoil under the canopy of *F. japonica* emerges from

339     our study. Thus, topsoil under *F. japonica* has 35% to 60% higher concentrations of Cu, K,

340     Mg, Mn, P and Zn. At some sites, even larger impacts have been found (e.g. 2-fold

341     increase in K and P at Ghi; 2.5-fold increase in Zn and Cu at EN). Large impacts on topsoil

342     chemistry have been well documented for trees (e.g. Musil, 1993; Finzi *et al.*, 1998a, b;

343     Augusto *et al.*, 2002; Hagen-Thorn et al., 2004) but seem more unusual for herbaceous

344     species. A few herbaceous invasive species however have been found to have strong

345     impacts on cations and phosphorus bioavailability (Blank & Young, 2002; Duda *et al.*,

346     2003; Vanderhoeven *et al.*, 2005; Chapuis-Lardy *et al.*, in press). For instance, K, Mg and

347  Ca were 3 to 6 times more abundant in the soil solution of soils invaded by *Lepidium*

348  *latifolium* (Blank & Young, 2002). Most of the time, the invasion has an important impact

349  on few elements (P, K, Na for *Halogeton glomeratus* (Duda *et al.*, 2003), P for *Solidago*

350  *gigantea* (Chapuis-Lardy *et al.*, in press)). To our knowledge, our study is one of the first

351  to demonstrate large impacts of a herbaceous invasive species on many elements in a

352  relatively large number of sites.

353      The six sites sampled in this study span a very broad range of soil chemical conditions

354  and floristic composition of resident plant community. *Fallopia japonica* can obviously

355  achieve high invasive success both in highly eutrophicated sites (For: extremely high

356  concentrations of bioavailable P) as well as in sites with much lower concentrations of

357  mineral nutrients (e.g. VK). Several authors already mentioned the broad range of soil

358  conditions tolerated by *F. japonica*. In UK, it has been found on soil with pH ranging from

359  3.0 to 8.0 (Grime *et al.*, 1988). Beerling *et al.*, (1994) found *F. japonica* on soils with very

360  different fertility levels (P: 1 - 60 mg kg$^{-1}$, K: 31 - 257 mg kg$^{-1}$).

361

362  Enhanced nutrient uptake rates

363

364  Plant-driven alterations of topsoil chemical composition can be due to changes in mineral

365  nutrient fluxes in the plant-soil system. (Ehrenfeld *et al.*, 2001; Blank & Young, 2002).

366  Increased nutrient concentrations in topsoil fits in well with our finding of enhanced

367  mineral nutrient cycling rates in invaded plots. In *Lepidium latifolium*, increased topsoil

368  concentrations of several nutrients could be ascribed to correspondingly higher

369  concentrations of these nutrients in tissues (Blank & Young, 2002; Duda *et al.*, 2003). A

370  similar mechanism cannot be invoked here because *F. japonica* has lower tissue nutrients

371  concentrations. Thus, mineral element composition of debris cannot in itself explain

372    increased nutrient pools in topsoil. However, low tissue concentrations are

373    overcompensated for by 3- to 13-fold higher aboveground biomass production. Lower

374    concentrations of nutrients can arguably indicate higher nutrient use efficiency (Vitousek,

375    1982). In other words, producing 1 g dry matter of *Fallopia* requires lower amounts of

376    nutrients compared to native vegetation. In this study, tissue concentrations refer to whole

377    shoot. Low concentrations of nutrients in *Fallopia* might be ascribable to the high biomass

378    allocation to nutrient-poor stems. Our data do show much lower concentrations of nutrients

379    in stems compared to leaves: *F. japonica* allocates approximately 68% of its aerial biomass

380    to stems poor in Mg (590 mg kg$^{-1}$), Mn (25 mg kg$^{-1}$) and to a lesser extent in P (1489 mg

381    kg$^{-1}$), Zn (27 mg kg$^{-1}$) and N (0.6%) compared to the 32% of the biomass invested in

382    nutrient-rich leaves (Mg: 5264 mg kg$^{-1}$, Mn: 263 mg kg$^{-1}$, P: 2518 mg kg$^{-1}$, Zn: 54 mg kg$^{-1}$

383    and N: 2.6%) (Dassonville, unpubl. data).

384    We have not measured nutrient resorption from senescing leaves and stems in this

385    study. Nutrient fluxes in litterfall are most likely smaller than annual nutrient uptake for

386    shoot construction. However, this holds true for both invaded and uninvaded stands.

387    Therefore, it is safe to conclude that the amounts of nutrients returned annually to soil in

388    litterfall are much higher in plots invaded by *Fallopia* compared to the resident vegetation.

389    According to Prescott (2002), total nutrient return via litter fall is the best predictor (better

390    than litter chemistry, e.g. C/N, lignin/N) of the effect of a plant species on nutrient

391    availability in the soil. Enhanced fluxes of nutrients may thus result in increased

392    availability of the corresponding nutrients in topsoil, by the mechanism of nutrient uplift

393    (Jobbagy & Jackson, 2004). Thus, if *F. japonica* obtains a significant proportion of mineral

394    nutrients from deeper soil layers, compared to the resident vegetation, biogeochemical

395    cycling of nutrients will result in net displacement of nutrients from deep layers to topsoil.

396    *F. japonica* does indeed have very deep rooting depth. Its rhizome system can grow up to 2

397    meter in depth (Child *et al.*, 2001). Nutrient uplift is a well known mechanism for trees.

398    For instance, Ca pumping from deep soil explained the higher Ca availability under the

399    canopy of *Acer saccharum* compared to that of *Tsuga canadensis* (Dijkstra & Smits,

400    2002). The same mechanism has been invoked to explain elevations of P and Ca under the

401    canopy of the invasive herbaceous *Lepidium latifolium* (Blank & Young, 2002). It is

402    interesting to notice that nitrogen does not follow the same pattern as metallic elements,

403    likely because most of it is taken up from topsoil.

404

405    Homogenization effects

406

407    Beside these general trends, our study reveals pervasive site-specific effects (i.e. significant

408    site x invasion interaction in the two-way ANOVA). Variation in impacts of *F. japonica*

409    across sites apparently follows a clear pattern. Thus, in contrast to the general trends, sites

410    with the highest values of any particular element in uninvaded plots systematically show

411    decreased values of that element in invaded plots. This holds true for Cu (HAR), K (FOR),

412    Mg (FOR), P (FOR), Zn (HAR), N (FOR) and organic matter (GHI). pH and Mn are the

413    only exceptions to that pattern. In contrast, those sites with the lowermost values in

414    uninvaded plots systematically show increased values in invaded plots (pH: VK, Cu: GBX;

415    K: VK; Mg: VK; P: all sites except For; Zn: GBX; N: GBX; organic matter: GBX; C/N:

416    GBX).

417    This hypothesis has been tested by doing a linear regression between uninvaded values and

418    the difference between invaded and uninvaded values or on log transformed data when the

419    data were not normally distributed and it was the case for Cu, Zn and P (figure 1). The

420    slope of these regression lines was always negative (confirming the homogenization

421    hypothesis) except for Mn and this was significant for Cu, C and N and close to

422 significance (0.05<p<0.10) for K and C/N. This pattern can be interpreted as a

423 convergence of invaded plots towards similar values of soil parameters. It has been

424 proposed that alien invasive species may result in floristic homogenization of landscapes

425 (Olden & Poff, 2003; McKinney, 2004). To our knowledge, this study is the first to

426 demonstrate such homogenizing effects on soil conditions. Thus, variation range of

427 element concentrations across sites was systematically narrower in invaded plots than in

428 uninvaded ones, most strikingly so for Cu (6.8-fold variation among resident plots vs. 2.4-

429 fold in invaded plots); K (4.1-fold vs. 2.6-fold), P (33.6-fold vs. 10.8-fold), Zn (7.6-fold vs.

430 2.7-fold), N (2.7-fold vs. 1.5-fold), C (3.7-fold vs. 1.8-fold) (Figure 1).

431

432 Soil organic matter

433

434      Despite increased productivity and litterfall, the impact on soil organic carbon was not

435 large. Two explanations can be put forward. First, litter was not sampled in this study and

436 it is thus possible that invaded plots actually have increased amounts of litter. Secondly,

437 unchanged or decreased (GHI and FOR) concentrations of organic C may be due to

438 enhanced mineralization rate. Clearly, a careful study of litter decomposition dynamics is

439 required to clarify this issue.

440

441 Inhibition of succession?

442

443 In its native range, *Fallopia japonica* is a pioneer species that facilitates the establishment

444 of later successional native species including *Miscanthus oligostachyus* and *Aster*

445 *ageratoides* (Hirose & Tateno, 1984). There, late successionals establish in gaps which

446 appear naturally in the centre of the old clones of *F. japonica* (Adachi *et al.*, 1996). This

447 phenomenon is known as "central die-back" (Adachi *et al.*, 1996). In contrast, central die-

448 back of *F. japonica* clones does not seem to have been observed in the introduction area.

449 Furthermore, in Western Europe, *F. japonica* usually forms very dense, monospecific

450 stands (Beerling *et al.*, 1994) and there is no study documenting the invasion of *F.*

451 *japonica* patches by other species (whether native or alien). Even in large old patches (>

452 400 m$^2$) in the site "GHI", no tree or shrub has yet been able to establish (Dassonville,

453 pers. obs.). It would appear that *F. japonica* may actually inhibit succession as reported for

454 the invasive *Ligustrum sinense* in the USA (Merriam and Feil, 2002). This phenomenon

455 could be explained by a positive feedback: plant-driven alterations of soil properties may

456 enhance growth or survival of the species or favor its self-replacement. For instance,

457 *Mesembryanthemum crystallinum* accumulates salt in the topsoil which prevents growth of

458 nontolerant species and subsequently increases its own success in the invaded site (Vivrette

459 & Muller, 1977). In the experiment of Blank and Young (2004), three invasive plants

460 (*Centaurea solstitialis*, *Lepidium latifolium* and *Bromus tectorum*) were cultivated in pots.

461 After three years, the availability of specific mineral nutrients increased in soil and plants

462 showed higher growth and nutrient uptake demonstrating a positive feedback effect.

463 Whether a similar mechanism contributes to the high invasive success of *Fallopia japonica*

464 should be investigated.

465  In conclusion, *Fallopia japonica* has long been considered as one of the most

466 troublesome alien invasive species in Europe, due to its dramatic effects on plant

467 community structure. This work indicates that it also has profound effects on ecosystem

468 processes. The relevance of these impacts to management should be investigated. In

469 particular, restoration of vegetation might be hampered by long term alterations of topsoil

470 properties.

471

472 **Acknowledgements**

473

478

479

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614

615　**Table I** Site denomination, localization and characterization of the invaded habitat.

616

| Site denomination | Localization | geographic coordinates | Type of habitat |
|---|---|---|---|
| **EN** | Enfants noyés | 50°47'31"N 4°24'30"E | Forest pond bank |
| **VK** | Forêt de Soignes | 50°47'10"N 4°25'3"E | Beech Forest |
| **Gbx** | Gembloux | 50°34'20"N 4°42'42"E | Cultivated field margin |
| **Har** | Haren | 50°23'13"N 4°26'30"E | Rough grassland |
| **For** | La Foresterie | 50°47'11"N 4°25'15"E | Wasteland |
| **Ghi** | Les Marionvilles | 50°27'30"N 3°50'25"E | Rough grassland |

617

618 **Table II** Phytosociological table of invaded (I) and control uninvaded (U) plots.

| | Har I | For I | Ghi I | Gbx I | VK I | EN I | EN U | Har U | Ghi U | VK U | Gbx U | For U |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Number of species** | 1 | 1 | 1 | 4 | 4 | 6 | 10 | 9 | 24 | 12 | 4 | 5 |
| *Fallopia japonica* | 5 | 5 | 5 | 5 | 5 | 4 | | | | | | |
| *Circea lutetiana* | | | | | + | | | | | | | |
| *Glechoma hederacea* | | | | | | 2 | 2 | | 1 | | | |
| *Petasites hybridus* | | | | | | + | 5 | | + | | | |
| *Carex pendula* | | | | | | 2 | 2 | | | | | |
| *Chrysosplenium oppositifolium* | | | | | | + | 2 | | | | | |
| *Cardamine hirsuta* | | | | | | | 1 | | | | | |
| *Chrysosplenium alternifolium* | | | | | | | 2 | | | | | |
| *Geum urbanum* | | | | | | | + | | | | | |
| *Angelica sylvestris* | | | | | | | + | | | | | |
| *Ranunculus repens* | | | | | | | + | | | | | |
| *Heracleum sphondylium* | | | | + | | | | 1 | | | | |
| *Tanacetum vulgare* | | | | | | | | 1 | | | | |
| *Vicia cracca* | | | | | | | | + | | | | |
| *Agrostis capillaris* | | | | | | | | 2 | 2 | | | |
| *Arrhenatherum elatius* | | | | | | | | 3 | 2 | | | |
| *Dactylis glomerata* | | | | | | | | 2 | + | | | |
| *Cirsium arvense* | | | | | | | | 3 | 1 | + | | 1 |
| *Urtica dioica* | | | | + | 1 | + | 1 | 2 | + | + | 4 | 5 |
| *Rubus sp.* | | | | + | | | | | 2 | 3 | 2 | 1 |
| *Calamagrostis epigejos* | | | | | | | | | 3 | | | |
| *Clinopodium vulgare* | | | | | | | | | 2 | | | |
| *Achillea millefolium* | | | | | | | | | 3 | | | |
| *Eupathorium cannabinum* | | | | | | | | | 2 | | | |
| *Festuca rubra* | | | | | | | | | 2 | | | |
| *Hypochoeris radicata* | | | | | | | | | 2 | | | |
| *Mentha sp.* | | | | | | | | | 1 | | | |
| *Carex hirta* | | | | | | | | | 1 | | | |
| *Daucus carota* | | | | | | | | | 1 | | | |
| *Cerastium fontanum* | | | | | | | | | + | | | |
| *Clematis vitalba* | | | | | | | | | + | | | |
| *Hypericum perforatum* | | | | | | | | | + | | | |
| *Rosa canina* | | | | | | | | | + | | | |
| *Senecio jacobea* | | | | | | | | | + | | | |
| *Symphytum officinale* | | | | | | | | | + | | | |
| *Vicia sativa* | | | | | | | | | + | | | |
| *Rumex crispus* | | | | | | | | | | + | | |
| *Deschampsia cespitosa* | | | | | | | | | | 2 | | |
| *Dryopteris dilatata* | | | | | | | | | | 2 | | |
| *Juncus effusus* | | | | | | | | | | 2 | | |
| *Lycopus europaeus* | | | | | | | | | | 1 | | |
| *Polygonum hydropiper* | | | | | | | | | | + | | |
| *Lotus pedunculatus* | | | | | | | | | | + | | |
| *Epilobium ciliatum* | | | | | | | | | | + | | |
| *Athyrium filix-femina* | | | | | 1 | | | | | + | | |
| *Calystegia sepium* | | | | | | | | | | | 1 | |
| *Galium aparine* | | | | | | | | + | | | 2 | 1 |
| *Epilobium hirsutum* | | | | | | | | | | | | 1 |

619

620 The numbers are abundance-dominance coefficients of Braun-Blanquet.

621 **Table III** Element concentrations in plant tissues and nutrient stocks in standing biomass

622 in invaded (I) and uninvaded (U) plots at five sites.

623

| | | | Concentrations in plant tissues (mg kg$^{-1}$) | | | | | | | | | | Nutrient stocks in standing biomass (g m$^{-2}$) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Ca | Cu | K | Mg | Mn | P | Zn | C (%) | N (%) | C/N | Ca | Cu | K | Mg | Mn | P | Zn | C | N |
| EN | I | Mean | 17278 | 7.84 | 18932 | 2289 | 18.8 | 2477 | 41.85 | 43.81 | 1.43 | 31.3 | 29119 | 13.15 | 29278 | 3747 | 26.9 | 3998 | 63.07 | 726.3 | 22.9 |
| | | SD | 1480 | 1.03 | 3993 | 146 | 8.9 | 326 | 13.12 | 0.38 | 0.21 | 5.3 | 16699 | 7.44 | 9879 | 1768 | 11.3 | 1880 | 20.95 | 357.0 | 10.5 |
| | U | Mean | 22363 | 13.59 | 45681 | 4136 | 16.2 | 4913 | 26.36 | 37.92 | 2.20 | 17.3 | 8984 | 5.25 | 17184 | 1650 | 6.6 | 1871 | 10.16 | 149.4 | 8.6 |
| | | SD | 3447 | 1.35 | 9723 | 1132 | 3.9 | 663 | 1.78 | 0.53 | 0.02 | 0.3 | 4295 | 1.73 | 4444 | 804 | 3.7 | 526 | 3.10 | 56.8 | 3.2 |
| | | t-value | -3.32* | -8.29*** | -6.23*** | -3.96* | 0.65 | -8.08*** | 2.87 | 22.13*** | -8.82*** | 6.5*** | 2.86 | 2.53 | 2.73 | 2.64 | 4.19** | 2.67* | 6.12*** | 3.91* | 3.19* |
| Gbx | I | Mean | 6370 | 2.28 | 6576 | 1048 | 73.3 | 791 | 14.23 | 44.10 | 1.04 | 42.6 | 23918 | 8.56 | 25125 | 3863 | 256.5 | 2980 | 52.24 | 1667.2 | 39.3 |
| | | SD | 578 | 0.26 | 1045 | 367 | 81.0 | 71 | 5.79 | 0.22 | 0.07 | 2.7 | 2852 | 1.30 | 6232 | 1114 | 273.0 | 418 | 17.81 | 238.1 | 6.2 |
| | U | Mean | 8126 | 3.33 | 8834 | 1527 | 60.5 | 1283 | 21.01 | 41.58 | 1.85 | 23.7 | 5308 | 2.21 | 5626 | 997 | 40.8 | 845 | 13.71 | 280.0 | 12.0 |
| | | SD | 2247 | 0.31 | 2756 | 298 | 7.7 | 169 | 6.51 | 1.45 | 0.43 | 6.3 | 1578 | 0.53 | 1203 | 196 | 11.7 | 169 | 4.43 | 73.4 | 2.0 |
| | | t-value | -1.85 | -6.34*** | -1.88 | -2.48 | 0.38 | -6.56*** | -1.91 | 4.21** | -4.54** | 6.77*** | 13.98*** | 11.09*** | 7.52*** | 6.21*** | 1.93 | 11.62*** | 5.14** | 13.64*** | 10.28*** |
| Har | I | Mean | 11440 | 5.46 | 19023 | 1136 | 47.2 | 1620 | 62.89 | 44.21 | 1.11 | 40.1 | 26906 | 12.92 | 45368 | 2628 | 108.4 | 3901 | 146.30 | 1054.4 | 26.4 |
| | | SD | 1125 | 0.60 | 736 | 170 | 17.6 | 154 | 13.50 | 0.38 | 0.07 | 2.7 | 6774 | 3.72 | 13378 | 488 | 46.0 | 1313 | 38.59 | 311.4 | 7.7 |
| | U | Mean | 16584 | 7.39 | 19044 | 1234 | 55.4 | 2352 | 128.79 | 41.13 | 1.46 | 32.3 | 9925 | 3.93 | 11931 | 631 | 25.3 | 1294 | 64.83 | 229.5 | 7.4 |
| | | SD | 5431 | 1.65 | 6527 | 492 | 37.6 | 447 | 57.92 | 1.98 | 0.59 | 12.4 | 7123 | 1.66 | 10583 | 260 | 14.9 | 719 | 27.81 | 124.2 | 2.7 |
| | | t-value | -2.27 | -2.69 | -0.01 | -0.46 | -0.49 | -3.79* | -2.71 | 3.73* | -1.45 | 1.51 | 4.23** | 5.41** | 4.80** | 8.84*** | 4.21** | 4.27** | 4.19** | 6.03*** | 5.68*** |
| For | I | Mean | 6302 | 2.19 | 7239 | 618 | 11.7 | 877 | 14.37 | 44.50 | 1.09 | 41.0 | 17339 | 6.03 | 20183 | 1715 | 33.4 | 2435 | 39.30 | 1248.0 | 30.7 |
| | | SD | 609 | 0.15 | 724 | 96 | 5.4 | 57 | 1.21 | 0.56 | 0.10 | 3.9 | 5117 | 1.79 | 7553 | 586 | 18.8 | 827 | 10.54 | 478.6 | 12.1 |
| | U | Mean | 22072 | 6.52 | 21717 | 1644 | 26.6 | 3677 | 24.90 | 41.25 | 1.37 | 30.6 | 18186 | 5.47 | 18052 | 1370 | 22.6 | 3074 | 20.85 | 346.2 | 11.3 |
| | | SD | 4274 | 1.95 | 2396 | 441 | 12.3 | 301 | 3.94 | 0.58 | 0.16 | 4.1 | 1944 | 1.79 | 1333 | 384 | 11.2 | 367 | 3.98 | 43.5 | 0.7 |
| | | t-value | -8.95*** | -5.40** | -14.17*** | -5.57** | -2.72 | -22.39*** | -6.26*** | 9.85*** | -3.54* | 4.5** | -0.38 | 0.55 | 0.68 | 1.21 | 1.21 | -1.73 | 4.01* | 4.60** | 3.92* |
| Ghi | I | Mean | 5721 | 2.02 | 9394 | 661 | 4.9 | 644 | 12.22 | 44.02 | 0.83 | 53.7 | 23496 | 8.19 | 39046 | 2700 | 20.1 | 2643 | 48.97 | 1812.3 | 33.7 |
| | | SD | 711 | 0.21 | 1429 | 152 | 1.4 | 49 | 3.43 | 0.21 | 0.13 | 7.9 | 9617 | 3.00 | 18499 | 1064 | 8.8 | 1086 | 21.39 | 767.0 | 12.0 |
| | U | Mean | 6591 | 4.48 | 8016 | 869 | 15.6 | 1342 | 26.28 | 43.55 | 1.02 | 41.9 | 2049 | 1.42 | 2484 | 272 | 4.9 | 419 | 8.13 | 140.0 | 3.3 |
| | | SD | 2320 | 0.80 | 3107 | 300 | 2.2 | 248 | 8.46 | 2.68 | 0.10 | 4.2 | 709 | 0.35 | 894 | 98 | 0.9 | 58 | 2.09 | 32.9 | 0.6 |
| | | t-value | -0.88 | -7.27*** | 0.99 | -1.52 | -9.90*** | -6.77*** | -3.77* | 0.43 | -2.87 | 3.23* | 5.45** | 5.49** | 4.84** | 5.56** | 4.20** | 5.01** | 4.66** | 5.34** | 6.22*** |

624

625 Biomass could not be harvested in site VK. SD = standard deviation. Means are compared

626 by *t*-tests. * $P < 0.05$ ; ** $P < 0.01$ ; *** $P < 0.001$.

627 **Table IV** Two-Way ANOVA of mineral element concentrations in plant tissues and total nutrient

628 stocks in standing biomass.

629

| | d.f. | Ca | Cu | K | Mg | Mn | P | Zn | C | N | C/N |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Concentrations in plant tissues** | | | | | | | | | | | |
| Site | 4 | 51.20*** | 160.86*** | 64.01*** | 50.48*** | 16.83*** | 222.43*** | 71.12*** | 5.63*** | 3.56* | 24.38*** |
| Invasion | 1 | 48.55*** | 243.06*** | 39.04*** | 43.38*** | 10.17** | 516.17*** | 27.63*** | 153.34*** | 140.68*** | 68.21*** |
| Site X Invasion | 4 | 11.91*** | 12.65*** | 16.72*** | 5.41** | 2.22 | 33.02*** | 8.06*** | 5.30** | 2.53 | 1.51 |
| **Nutrient stocks in standing biomass** | | | | | | | | | | | |
| Site | 4 | 9.51*** | 11.43*** | 23.36*** | 20.69*** | 44.27*** | 10.19*** | 22.27*** | 10.36*** | 11.12*** | |
| Invasion | 1 | 69.55*** | 161.98*** | 51.98*** | 136.49*** | 237.44*** | 99.94*** | 54.13*** | 394.62*** | 282.36*** | |
| Site X Invasion | 4 | 2.54 | 21.35*** | 1.76 | 18.62*** | 8.08*** | 8.43*** | 2.61* | 5.94** | 9.69*** | |

630

631 N = 5 sites for all parameters. *F* values and significance level: * $P < 0.05$ ; ** $P < 0.01$ ; *** $P <$

632 0.001.

633 **Figure 1** Linear regression between soil chemical parameters in uninvaded plots (U) and

634 difference between invaded and uninvaded plots (I-U) at 6 sites (or on log transformed data

635 when normality was not respected: Cu, Zn, P). Values are in mg kg$^{-1}$ except for C and N

636 (in %) Whiskers are standard error. Values of I-U (or Log I-Log U)>0 indicate an increase

637 of the element availability in the invaded soil. Values <0 indicate a decreased availability.

638 When significant the increase/decrease is marked with the significance level of the t-test (*

639 $P < 0.05$ ; ** $P < 0.01$ ; *** $P < 0.001$). The results of the two-way ANOVA are indicated:

640 $F$ values and significance level.

641

642 **Figure 2** Comparison of soil properties between invaded and uninvaded plots expressed as

643 the ratio of mean value of invaded plots on mean value of uninvaded plots (I/U). N = 6

644 sites for all parameters. Whiskers are standard error. The horizontal line (I/U=1) denotes

645 equal value for invaded and control plots. Value above the line (I/U>1) indicates increased

646 value in invaded plots. Significance level of Invasion effect in the two-way ANOVA: * $P <$

647 0.05 ; ** $P < 0.01$ ; *** $P < 0.001$.

648

649 **Figure 3** Biomass (Mass), element concentrations in biomass, mineral nutrient stocks in

650 aboveground biomass. Comparison of invaded (I) and uninvaded (U) plots expressed as the

651 ratio I/U : biomass (hatched), element concentrations in plant tissues (lines) and mineral

652 nutrient stocks in standing biomass (white). N = 5 sites for all parameters. Whiskers are

653 standard errors. The horizontal line (I/U = 1) denotes equal value for invaded and

654 uninvaded plots. Significance level of Invasion effect in the two-way ANOVAs. * $P < 0.05$

655 ; ** $P < 0.01$ ; *** $P < 0.001$.
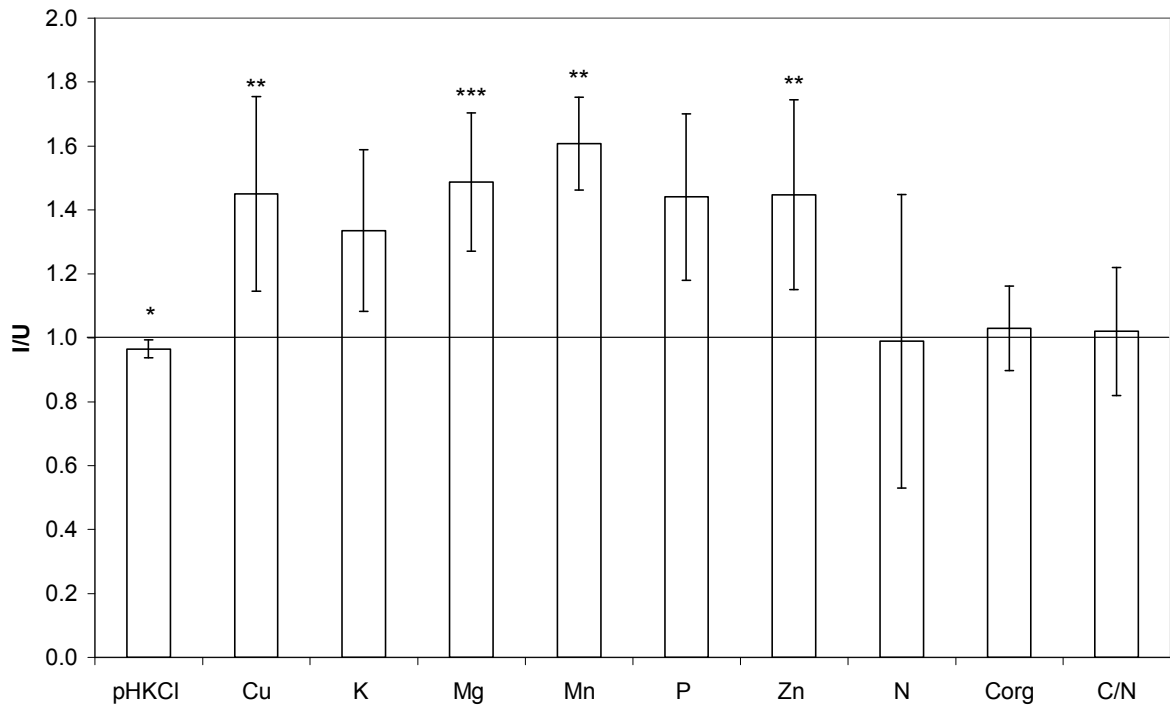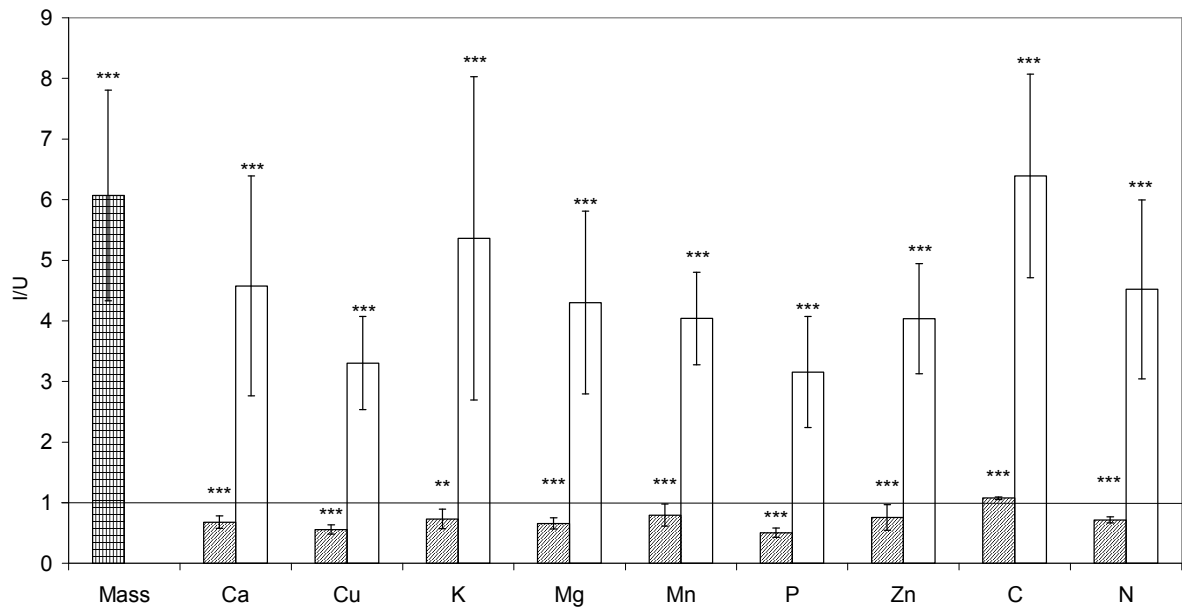
656     Figure 1
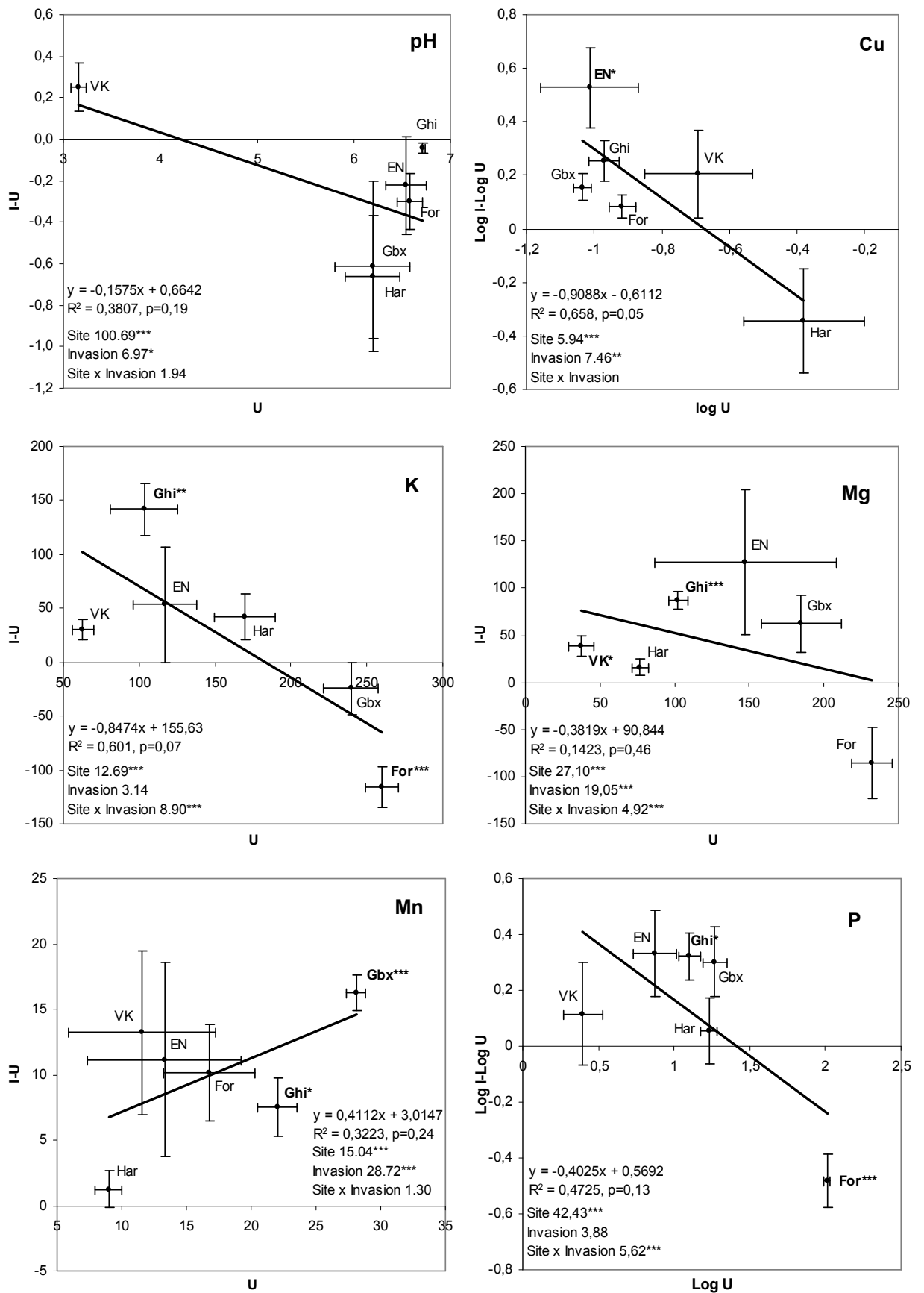


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658     Figure 1
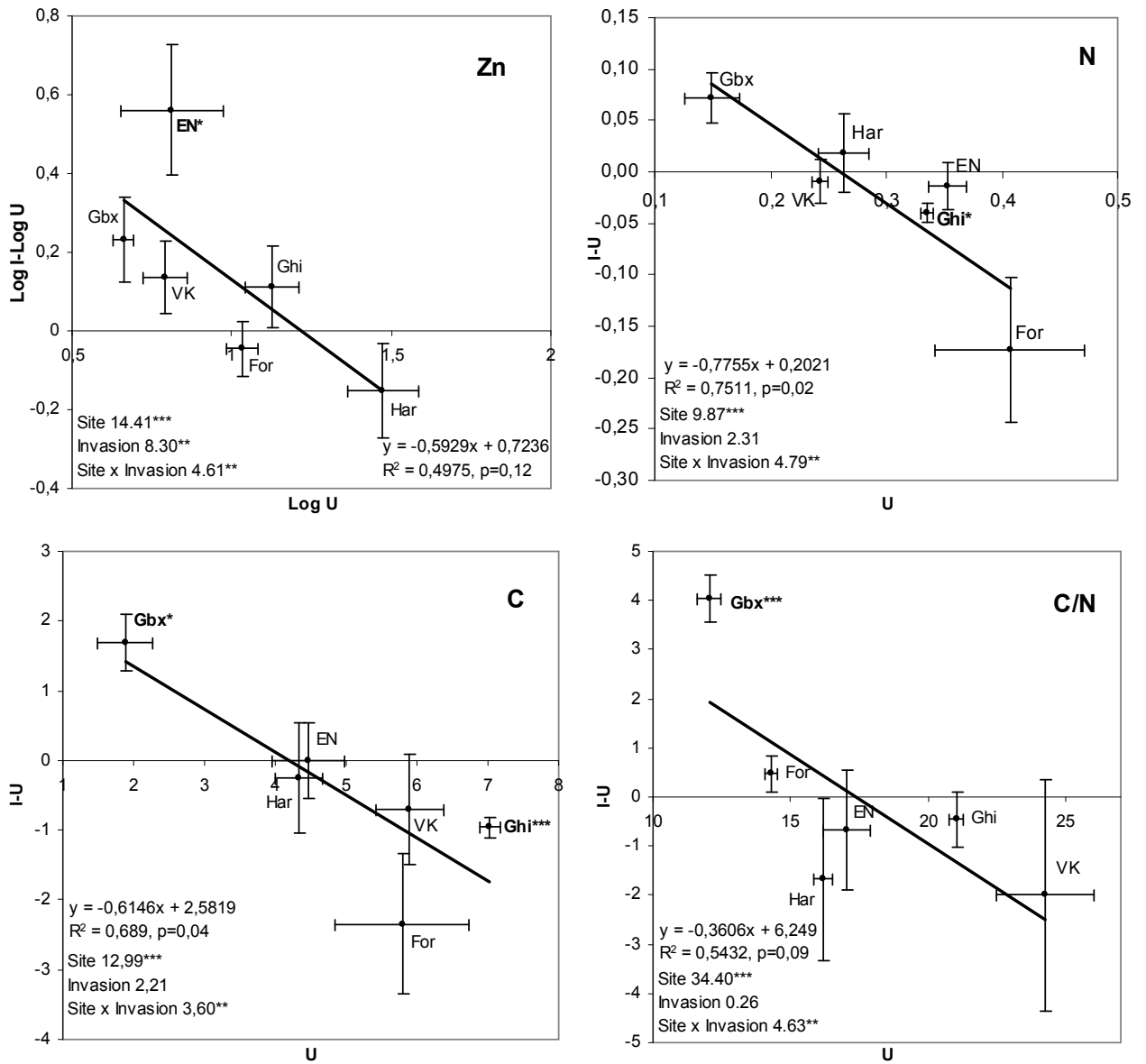


659

660    Figure 2



661

662    Figure 3



663

664