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Thesium linophyllum parasitizes expansive Calamagrostis epigejos and restricts its dominance in a long-term vegetation survey

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Running title

Thesium linophyllum's effect on *Calamagrostis epigejos*

Keywords

Biological control; clonal grass; conservation management; haustorium; landfill restoration; species rich grassland

Abstract

- Root-hemiparasitic interaction between the dominant grass *Calamagrostis epigejos* and hemiparasitic *Thesium linophyllum* was studied to assess the potential of the parasite to regulate dominance of the grass expanding into species rich steppe grasslands.
- First, we aimed at identification of physiological links between the two species, as a principal indicator of the parasitic relationship. Second, we analysed the dynamics of the two species in a steppe grassland at the foot of the Bükk Mountains, Hungary,

where their joint presence is recorded in a long-term permanent-plot monitoring dataset to detect a pattern associated with the parasitic ecological interaction.

- Numerous well-developed functional haustoria of *Th. linophyllon* were identified on the root systems of *C. epigejos*. The joint dynamics of *C. epigejos* and *Th. linophyllon* displayed clear signs of the parasitic interaction: 1. The dynamics of *Th. linophyllon* frequency was positively associated with the initial cover of *C. epigejos*. 2. Maximal recorded cover values of the two species were strongly positively correlated and 3. The extent of *C. epigejos* decrease in the vegetation was significantly positively associated with maximum *Th. linophyllon* cover recorded throughout the monitoring period.
- We demonstrate that *C. epigejos* can be parasitized by *Th. linophyllon* which restricts its abundance. *Th. linophyllon* thus has a potential to act as a native biological control of *C. epigejos* in steppe grasslands.

Nomenclature: Tutin et al. (1964-1993).

1 **Introduction**

2 *Calamagrostis epigejos* is a range-expanding grass spreading into natural and seminatural
3 grasslands in Central Europe (Rebele & Lehmann 2001). This expansion is one of the most
4 prominent factors threatening biodiversity of these highly diverse communities. *C. epigejos* is
5 a clonal species displaying guerila clonal strategy to colonize previously unoccupied plots
6 (Klimešová & de Bello 2009). Consequently and thank to its tall habit it often attains
7 dominance. *C. epigejos* produces a thick layer of slowly decomposing litter which has a
8 strong suppressive effect on other species (Rebele & Lehmann 2002). As a result,
9 competitively weaker species are excluded from the community, which decreases its diversity
10 (Somodi *et al.* 2008; Rebele 2014).

11 Standard conservation management of *Calamagrostis epigejos*-infested grasslands includes
12 intense mowing (twice a year or more; Lehmann & Rebele 2002). While such management
13 can indeed suppress the grass, it may also have negative effect on the rest of the community.
14 In steppe grasslands, species with late phenology (e.g. *Aster amellus*, *Aster linosyris*,
15 *Odontites luteus*) and characteristic *Stipa* grasses may react negatively to mowing. Moreover,
16 intense mowing is laborious and costly in particular considering the difficult terrain on which
17 these communities are often located. Recently, introduction of hemiparasitic *Rhinanthus*
18 species (Orobanchaceae) was suggested as an alternative or complement to mowing (Těšitel
19 *et al.* 2017). These parasitic plants parasitize *C. epigejos* inflicting a massive damage. As a
20 result, *C. epigejos* may be exterminated from the community in short term while the
21 characteristic species composition is restored (Těšitel *et al.* 2017). *Rhinanthus* spp. as
22 biocontrol agents are however of limited use in steppe grasslands. They are rather rare in
23 these communities (Těšitel *et al.* 2015a) due to the sensitivity of their seedlings to drought
24 (Ameloot *et al.* 2006) and specialized physiology characterized by wasting water (Jiang *et al.*
25 2003).

26 There are nevertheless other root-hemiparasitic plants which inhabit steppe grasslands.
27 *Thesium linophyllum* (Thesiaceae, Santalales) is a clonal perennial herb (Klimešová & de
28 Bello 2009) typical of dry calcareous grasslands and steppes (Těšitel *et al.* 2015a). *Thesium*
29 *linophyllum* is an unselective generalist hemiparasite forming haustoria on all species in its
30 surrounding (Dostálek & Münzbergová 2010). Root hemiparasites are generally known to
31 alter competitive hierarchies in plant communities potentially increasing biodiversity if
32 suppressing dominant competitors (Westbury *et al.* 2006; Pywell *et al.* 2007; Mudrák & Lepš
33 2010). No such effect has however been reported for *Thesium linophyllum* yet.

34 Here, we use the inspection of anatomic structures and long term vegetation monitoring
35 data to explore the interaction between *Calamagrostis epigejos* and *Thesium linophyllum*. We
36 hypothesize that *Calamagrostis* can serve as a host for *Thesium* and that *Calamagrostis*
37 abundance may be reduced by presence of *Thesium*.

38

39 **Materials and Methods**

40

41 *Study Site*

42

43 Our analyses are based on long-term monitoring data collected in a fragment of a formerly
44 grazed, but still species-rich, grassland at the foot of the Bükk Mountains, Hungary (47°54' N,
45 20°35' E). The area is relatively dreir compared to other occurrences of *C. epigejos* with 600
46 mm annual rainfall and 9 °C mean annual temperature. For further details of site conditions
47 and species composition see also Virágh (1982) and Virágh & Fekete (1984).

48 A long-term monitoring followed initial experiments with herbicides in 1979 (Virágh
49 1987, 1989). These previous experiments changed the species composition of the treated plots
50 considerably in the early years, but the assemblages had completely regenerated by 1988

51 (Virágh 1989). The experimental area have been revisited since than in selected years with
52 various intervals.

53 *C. epigejos* appeared first in a control plot in 1983 and had acquired dominance on half of
54 the experimental area by 2002. There was strong directionality in its expansion: it started to
55 spread from a patch present before abandonment at the bottom of a small valley, close to the
56 study area. The pattern of experimental treatments, however, did not influence the spread
57 pattern of *C. epigejos*. *C. epigejos* greatly transformed species composition (Somodi *et al.*
58 2008), however unaffected plots largely retained their species composition as a species rich
59 grassland dominated *Festuca rupicola* with a slight shift towards *Danthonia alpina* co-
60 dominance. *Thesium lynophyllon* was present at the site from the start, elevated frequency was
61 found in 2002 already, but started to gain dominance after 2005.

62

63 *Sampling description*

64

65 The sampling design installed for the previous experiments was used later in the
66 monitoring. The experiments were carried out in 1 m × 1 m non-contagious plots arranged
67 systematically in a grid with 50 cm spaces (Virágh 1987). Each 1 m × 1 m plot was
68 subdivided into 25 20 cm × 20 cm subplots. From the originally 45 experimental plots we
69 choose plots for the current analysis, for which data was available for each of the studied
70 years: 2002-2005, 2013-2015 and at least one of the two species in focus was present with
71 higher than 1% cover in any year. This yielded 10 plots for considerations in our analysis. To
72 avoid errors potentially induced by treating adjacent 20 cm × 20 cm subplots as replicates and
73 to increase plot size, we merged the 4 subplots in each corner of each plot and used these in
74 the analysis. Thus we obtained four 40 x 40 cm quadrats within each plot which we consider
75 as independent observations hierarchically nested within plots.

76 Presence of haustorial connections between *Thesium linophyllum* and *Calamagrostis*
77 *epigejos* was examined by visual inspection of *Calamagrostis* root system after excavation.
78 Observed haustorial connections were cut out, washed in distilled water and fixed in 2.5%
79 glutaraldehyde phosphate buffer. Their transverse sections were subsequently prepared by
80 hand cutting for inspection under a light microscope. Presence of a xylem bridge in the
81 haustoria and host-parasite xylem contact were examined as indicators of haustorium
82 functionality (Cameron & Seel 2007).

83

84 *Vegetation data analysis*

85

86 The parasitic interaction between organisms is characterized by resource flow from the
87 host to the parasite. As a result the parasite should benefit from host presence or abundance.
88 By contrast, the host should be suppressed if parasite is present and with the level of
89 suppression being positively affected by parasite abundance. This relationship may be more
90 complicated in case of a hemiparasitic association but in environments where abiotic
91 resources are scarce (such as steppe grasslands) it should be largely retained (Těšitel *et al.*
92 2015b). To detect the signature of parasitic interaction between *Calamagrostis* and *Thesium*,
93 we formulated three null hypotheses corresponding to neutral interaction between the species,
94 which were subsequently tested by the data originating from the long-term vegetation survey:
95 H₀₁: *Thesium* frequency (presence/absence) and its dynamics in monitoring quadrats does not
96 depend on *Calamagrostis* cover. H₀₂: Maximal recorded cover of both species in individual
97 quadrats throughout the monitoring period are not correlated. H₀₃: *Calamagrostis* cover in
98 monitoring quadrat does not depend on the interaction between year and maximal *Thesium*
99 cover recorded throughout the monitoring period.

100 To test H_{01} , frequency (presence/absence) of *Thesium linophyllum* in quadrats across
101 individual sampling years was summarized in a contingency table. The table was analysed by
102 generalized estimating equations (GEE) with *Thesium* presence/absence as a binomial
103 response and year, initial *Calamagrostis* cover (in 2002) and their interaction as predictors.
104 The GEE assumed first order-autoregressive correlation among residuals within each
105 monitoring quadrat. This correlation structure is suitable for time series but it assumes a
106 continuous time series, which does not hold for our data. However, a trial fit of GEE with
107 unstructured correlation structure did not identify any major change of correlation structure
108 which would correspond to the gap in the time series. H_{02} was tested by Pearson correlation
109 coefficient between the maximum cover of *Thesium* and *Calamagrostis* recorded in individual
110 quadrats throughout the monitoring period. H_{03} was tested by a linear mixed effect model
111 containing *Calamagrostis* cover as response, year, maximal *Thesium* recorded cover in given
112 quadrat and their interaction as fixed effect categorical predictors and quadrat identity nested
113 within block as a random effect predictor. To graphically illustrate the association between
114 *Thesium* abundance and the trend in *Calamagrostis* cover, we constructed a series of
115 scatterplots displaying dependence of difference of *Calamagrostis* cover in actual year
116 compared to 2002 on *Thesium* cover recorded in actual year.

117 All cover data were square-root transformed prior to analysis to improve normality and
118 homoscedasticity of the residuals. Square root transformation was used due to presence of
119 zeros in the data. A priori defined Helmert contrasts (contrasting actual factor level to the
120 mean of previous levels) were used to assess differences between years. All analyses were
121 conducted in R, version 3.3.2 (R Core Team 2016) and R packages *nlme* (Pinheiro *et al.*
122 2014) and *geepack* (Højsgaard *et al.* 2006).

123

124 **Results**

125

126 Examination of *Calamagrostis epigejos* root systems revealed numerous *Thesium* haustoria
127 attached to both roots and rhizomes (Fig. 1a). Xylem bridge and xylem contact between the
128 host and parasite were identified in their anatomical structure (Fig 1b,c), which indicates
129 functionality of the haustorial connections.

130 The generalized estimating equations rejected H_{01} by demonstrating significant effects of
131 year, initial *Calamagrostis* cover and their interaction on actual *Thesium* frequency. The
132 frequency of *Thesium linophyllum* significantly increased throughout the monitoring period
133 (Table 1; GEE: $\chi^2_6 = 18.9$, $P = 0.004$). The most pronounced differences occurred between
134 2005 and 2013, when *Thesium* frequency increased from one third to almost two thirds of the
135 quadrats. *Thesium* presence was significantly positively associated with initial *Calamagrostis*
136 cover (GEE: $\chi^2_1 = 6.1$, $P = 0.010$). The interaction term (GEE: $\chi^2_6 = 21.9$, $P = 0.001$) indicates
137 that the dynamics of *Thesium* frequency in quadrats was affected by *Calamagrostis* cover at
138 the beginning of sampling period. The interaction coefficient was significantly negative in
139 2003 (Helmert contrast; est = -0.0212, Wald $z = 3.90$, $P = 0.048$), significantly positive in
140 2014 (Helmert contrast; est = 0.0077, Wald $z = 5.35$, $P = 0.021$), and marginally non-
141 significantly positive in 2015 (Helmert contrast; est = 0.0076, Wald $z = 3.70$, $P = 0.054$).

142 The correlation coefficient between the maximum cover of *Thesium* recorded throughout
143 the monitoring period and that of *Calamagrostis* was significantly positive (Pearson $r =$
144 0.443, $P = 0.007$), which rejected H_{02} .

145 H_{03} was rejected by a significant effect of the interaction between year and maximal cover
146 of *Thesium* recorded throughout the monitoring period on actual *Calamagrostis* cover (Table
147 2). The interaction coefficients were significantly negative in 2004 ($t_{2004} = -1.98$, $P = 0.049$),
148 2013 ($t_{2004} = -3.46$, $P = 0.001$), 2014 ($t_{2004} = -3.507$, $P = 0.001$) and 2015 ($t_{2004} = -2.92$, $P =$
149 0.023). In correspondence to the mixed -effect model, significant negative correlations

150 between actual *Thesium* cover and *Calamagrostis* cover difference compared to 2002 were
151 also observed in these years (Fig. 2).

152

153 **Discussion**

154

155 Functional haustorial connections between *Thesium linophyllum* and *Calamagrostis*
156 *epigejos* represent a strong indication of parasitic interaction between these two species. The
157 analyses of long-term vegetation data managed to reject all three null hypotheses which
158 assumed independent vegetation dynamics of the two species. *Thesium* frequency was found
159 to increase over the ten years period and the probability of emergence in previously
160 unoccupied quadrats was positively associated with *Calamagrostis* cover. There was also a
161 positive association between maximum recorded cover of *Thesium* and *Calamagrostis*. At the
162 same time, a significant decrease of *Calamagrostis* was positively associated with *Thesium*
163 cover. These results indicate, that *Thesium* benefitted from high *Calamagrostis* abundance,
164 while *Calamagrostis* was reduced by *Thesium* as expected in a host-parasite interaction. Still,
165 we admit that the evidence on parasitic interaction between the two species is only based on
166 observation which makes it weaker than evidence based on manipulative experiments.
167 Unfortunately, such experiments (e.g. experimental sowing) are extremely difficult to conduct
168 with *Thesium linophyllum* due to its very low germination rate (Dostálek & Münzbergová
169 2010).

170 The observed effect of *Thesium* on *C. epigejos* is rather moderate. It seems that the two
171 species can coexist in a long term. However, *Thesium* seems to be able to establish in *C.*
172 *epigejos* stands and decrease its dominance in the community. That is important for
173 maintaining and restoring steppe grassland biodiversity since the loss of biodiversity
174 following *C. epigejos* establishment is a slow process and most species perish only after *C.*

175 *epigejos* attains dominance (Somodi *et al.* 2008). Moreover, *Thesium linophyllum* has recently
176 been demonstrated to belong within top 5% species associated with high species richness in
177 the vegetation of the Czech Republic (Fibich *et al.* 2017). Therefore, promoting *Thesium*
178 abundance may have also other positive effects on diversity in addition to preventing *C.*
179 *epigejos* dominance. The use of (hemi)parasitic plants to suppress populations of
180 competitively strong dominants, either native or alien invasives, is an emerging topic in
181 applied plant ecology. Recent research has demonstrated drastic effects the parasitic plants on
182 their competitive hosts; e.g. *Pedicularis palustris* on *Carex acuta* (Decler *et al.* 2013),
183 *Cuscuta campestris* on *Mikania micrantha* (Yu *et al.* 2008) or *Rhinanthus alectorolophus* on
184 *Calamagrostis epigejos* (Těšitel *et al.* 2017). Our study indicating the less pronounced, yet
185 significant effect of *Thesium linophyllum* demonstrates that even moderate effects of parasitic
186 plants only detectable in a long term can have a value for biodiversity conservation and
187 restoration. In contrast to the above mentioned examples, it seems that *Thesium* does not
188 require a special management measure to establish in *C. epigejos* stand. Furthermore, *T.*
189 *lynophyllum* remains part of the community and thus can control even a future increase in *C.*
190 *epigejos* due to an unplanned fire for example, which is known to boost *C. epigejos* spread
191 (Rebele & Lehmann 2001, Deák *et al.* 2014).

192 The moderate effect of *Thesium linophyllum* on *Calamagrostis epigejos* is probably caused
193 by the structure of the santalean haustoria. These haustoria do not feature an open vascular
194 connection with the host xylem and the uptake of nutrients proceeds via a contact parenchyma
195 (Tennakoon *et al.* 1997; Hibberd & Jeschke 2001). That limits the amount of nutrients and in
196 particular water acquired from the host while the loss of water is probably the major
197 mechanism inflicting harm to the hosts of hemiparasites in dry habitats (Těšitel *et al.* 2015b).
198 In addition, *Thesium* is a clonal and perennial species (Klimešová & de Bello 2009).
199 Therefore, its strategy may be based on a conservative host use to secure host resources for

200 future vegetation seasons. This contrasts with the ecological behaviour of many annual
201 hemiparasites which need to maximize the resource acquisition from the host and create gaps
202 in the vegetation to facilitate their seedling establishment (Demey *et al.* 2015; Lepš & Těšitel
203 2015).

204

205 *Applications and Perspectives*

206

207 Our study indicates the potential of *Thesium linophyllum* to regulate local abundance of
208 competitive *Calamagrostis epigejos* in dry grassland. This effect may possibly be used in
209 nature conservation practice to reverse the biodiversity decline associated with *C. epigejos*
210 expansion. However, further research of *Thesium linophyllum* reproductive biology and
211 ecological requirements is needed to identify measures promoting its abundance and to
212 develop methods of introduction to unoccupied target sites. Subsequently, *Thesium*
213 *linophyllum* may be tested as a promising hemiparasitic species to colonize and increase
214 diversity of extreme habitats such as post-mining sites, which have a successional potential to
215 develop into steppe grasslands (Prach *et al.* 2013) but such development may be hindered by
216 *Calamagrostis epigejos* and other synanthropic grass dominance (Prach & Pyšek 2001).
217 *Thesium linophyllum* is native in Central and Eastern Europe (Meusel *et al.* 1965), where
218 possible target post-mining or post-industrial sites are available in abundance.

219

220

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222

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226
227

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320

321 **Table titles**

322

323 **Table 1.** Frequency of *Thesium linophyllum* in individual monitoring quadrats in the course of
324 the study period.

325 **Table 2.** Summary of linear mixed-effect model testing dependence of *Calamagrostis* cover
326 on maximum recorded *Thesium* cover in monitoring quadrats.

327

328 **Figure captions**

329

330 **Figure 1.** Morphology and anatomy of *Thesium linophyllum* haustoria attached to
331 *Calamagrostis epigejos* roots. (a) Outer morphology of the haustoria. (b) Cross-section of the
332 haustorium attached to the host root (c) Details of the xylem contact between the host and the
333 parasite. Ha: Haustorium, HR: Host root, PR: Parasite root, VC: Vascular core of the
334 haustorium, XB: Xylem bridge, HB: Hyaline body, PXY: Parasite xylem, HXY: Host xylem.

335 **Figure 2.** Trends in *Calamagrostis epigejos* abundance displayed by cover difference
336 compared to 2002 at individual monitoring quadrats in 2003-2005 and 2013-2015. Regression
337 line is displayed for significant relationships. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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