Thesium linophyllon parasitizes expansive Calamagrostis epigejos and restricts its dominance in a long-term vegetation surve

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Running title
Thesium linophyllon'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 linophyllon* 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).

Introduction

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

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

26   There are nevertheless other root-hemiparasitic plants which inhabit steppe grasslands.

27   *Thesium linophyllon* (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   *linophyllon* 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 linophyllon 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 linophyllon*. 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 linophyllon* 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    $H0_1$: *Thesium* frequency (presence/absence) and its dynamics in monitoring quadrats does not

96   depend on *Calamagrostis* cover. $H0_2$: Maximal recorded cover of both species in individual

97   quadrats throughout the monitoring period are not correlated. $H0_3$: *Calamagrostis* cover in

98   monitoring quadrat does not depend on the interaction between year and maximal *Thesium*

99   cover recorded throughout the monitoring period.

6

100   To test $H0_1$, frequency (presence/absence) of *Thesium linophyllon* 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. $H0_2$ was tested by Pearson correlation

109   coefficient between the maximum cover of *Thesium* and *Calamagrostis* recorded in individual

110   quadrats throughout the monitoring period. $H0_3$ 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 $H0_1$ by demonstrating significant effects of

131   year, initial *Calamagrostis* cover and their interaction on actual *Thesium* frequency. The

132   frequency of *Thesium linophyllon* 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 $H0_2$.

145    $H0_3$ 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 linophyllon* 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 linophyllon* 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 linophyllon* 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* (Decleer *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 linophyllon* 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 *lynophyllon* 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 linophyllon* 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 linophyllon* 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 linophyllon* 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   *linophyllon* 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 linophyllon* 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.

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220

221   **Acknowledgements**

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228   **References**

229

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320

Table titles

Table 1. Frequency of *Thesium linophyllon* in individual monitoring quadrats in the course of the study period.

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

Figure captions

Figure 1. Morphology and anatomy of *Thesium linophyllon* haustoria attached to *Calamagrostis epigejos* roots. (**a**) Outer morphology of the haustoria. (**b**) Cross-section of the haustorium attached to the host root (**c**) Details of the xylem contact between the host and the parasite. Ha: Haustorium, HR: Host root, PR: Parasite root, VC: Vascular core of the haustorium, XB: Xylem bridge, HB: Hyalline body, PXy: Parasite xylem, HXy: Host xylem.

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