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Effects of tree characteristics and climatic conditions on gall midge abundance on European beech (*Fagus sylvatica* L.)

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Abstract: As a consequence of climate change and damage to coniferous forests, European beech (*Fagus sylvatica* L.) is the preferred plant species for forest restoration in Central Europe. European beech is generally regarded as pest-resistant. However, its vulnerability to secondary pests, for instance, gall-forming midges, may increase with environmental stress such as long drought periods. We analysed the abundance of two gall-forming insects, *Mikiola fagi* and *Hartigiola annulipes*, on European beech at 26 forest sites across the Czech Republic, spanning diverse climatic and environmental conditions, using generalised linear mixed models to evaluate the effects of abiotic factors and host tree characteristics. The results revealed that *M. fagi* was more abundant on younger trees, in stands with lower canopy closure, and under warmer spring conditions. In contrast, the abundance of *H. annulipes* declined in drought-affected areas. These patterns demonstrate species-specific responses of gall midges to host tree characteristics and climatic variables, suggesting that climate change may favour higher *M. fagi* abundance. Accordingly, our findings support the establishment of young beech stands under higher canopy closure, for example, beneath the shading of mature trees.

Keywords: climate change; damage; drought; pest; phenology; tree properties

The vitality and resilience of many Central European forests are threatened by the increasing frequency of prolonged droughts and higher temperatures, driven by climate change. Coniferous species are highly susceptible to pests and diseases under such conditions (Lorenc 2023; Knížek et al. 2023). Consequently, European beech (*Fagus sylvatica* L.) is widely used for forest regeneration, primarily due to its proven lower vulnerability to various stressors compared to other tree species (Černý et al. 2024; MoA 2024). However, this resilience may have been reduced by ongoing changes in air temperature and precipitation patterns (Machar et al. 2017). According to the Intergovernmental Panel on Climate Change (IPCC), the 1.5 °C warming threshold is likely to be exceeded within

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this decade. This is expected to accelerate climate change, leading to an increase in temperatures and alterations in precipitation, resulting in more frequent droughts (Lee, Romero 2023).

As the beech tree is known to be sensitive to drought (Frei et al. 2022), its health is likely to worsen in European regions (Machar et al. 2017; Langer et al. 2023). Similar to other tree species, beech trees affected by drought stress become more susceptible to pest infestations. Climate change can exacerbate this, as many insects benefit from longer growing seasons while host tree resistance is simultaneously reduced (Rouault et al. 2006; Walter et al. 2018). Although the European beech in Central Europe is not currently affected by major pest species (Černý et al. 2024), secondary pests can still cause serious damage. Such damage may even lead to mortality, particularly in trees already weakened by environmental stressors (Jactel et al. 2012).

In Central Europe, gall-forming midges, such as *Mikiola fagi* (Hartig, 1839) and *Hartigiola annulipes* (Hartig, 1839) (Diptera: Cecidomyiidae), are common secondary pests of beech trees (Skrzypczyńska 2008; Fernandes et al. 2003; Skuhravá et al. 2014). Outbreaks of *M. fagi* have been historically reported in several European countries, including Poland, Germany, and Romania (Skuhravá, Skuhravý 1974; Călărășanu, Chira 2013; Skuhravá et al. 2014). Similarly, *H. annulipes* can act as a local pest (Skrzypczyńska 2008; Skuhravá, Roques 2000).

These two gall-forming insects induce gall formation by altering the tissues of the host plant and creating new meristematic structures (Ferreira et al. 2022). Gall formation modifies the physiology, biochemistry, and morphology of the host plant, ultimately reducing its vitality and fitness (Pilichowski, Giertych 2020; Molnár et al. 2018). In addition, these gall midges diminish the effective leaf surface area, weaken growth, and increase vulnerability to additional pest attacks (Urban 2000a; Gossner et al. 2014).

Despite their potential impact, gall-forming insects often receive less attention than other forest pests (Gossner et al. 2014). Existing knowledge about the habitat preferences of the two gall-forming insects, *M. fagi* and *H. annulipes*, remains inconsistent, possibly due to regional climatic differences. To fill this knowledge gap on these two species, the present study aims to address the following research questions: (*i*) What is the influence of host tree characteristics (tree diameter, canopy closure, damage, biotic stress) on the abundance of *Mikiola fagi* and *Hartigiola annulipes*? (*ii*) How do critical climatic variables, particularly spring temperatures and precipitation deficits indicative of drought, affect the gall abundance of these two species? (*iii*) Do these two gall midge species exhibit distinct, species-specific responses to these environmental and host-related factors?

MATERIAL AND METHODS

Galls and environmental parameters. A total of 26 experimental sites were selected across the Czech Republic [Figure 1; Table S1 in the Electronic Supplementary Material (ESM)], with mean annual temperatures ranging from 6.3 °C to 10.8 °C and total annual precipitation between 541 and 1 103 mm (Table S1 in the ESM). The studied stands consisted primarily of planted trees, although natural regeneration was also frequently observed. The sites showed no evidence of recent management interventions, such as the presence of fresh stumps. At each site, 21–30 individuals of European beech were sampled (total $N = 662$). To ensure consistent and feasible sampling, we purposively selected the single branch on each tree that most accurately corresponded to a southern exposure, up to a maximum height of 2 m above ground. This approach, focusing on accessible branches from the lower canopy, is a common practice in entomological studies where comprehensive canopy sampling is logistically challenging (Gregoire et al. 1995; Ryall et al. 2011). Field surveys were conducted in September 2022.

Several additional characteristics were recorded for each tree and site. The presence of biotic stress was evaluated for each tree as a binary (presence/absence) variable. A tree was assigned as stress present if any visible symptoms of current or recent insect or pathogen activity were observed. These symptoms included, but were not limited to, insect boring holes, lesion exudates, significant fungal fruiting bodies, or distinct pathogenic cankers. For the entire dataset, 428 trees showed no signs of biotic stress, while 234 trees exhibited symptoms of biotic stress. These binary values were subsequently entered into the generalised linear mixed models (GLMMs) as a categorical predictor. Similarly, the 'tree damage' variable was assessed as a binary (presence/absence) categorical

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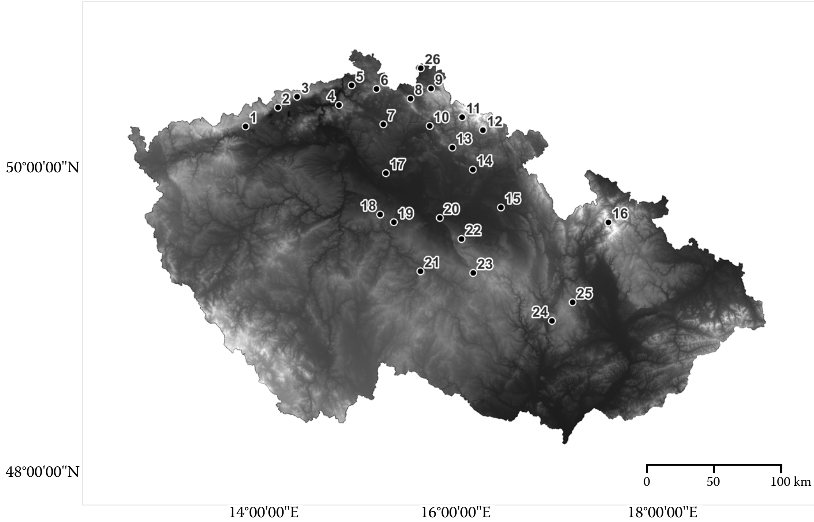

Figure 1. Map of the 26 selected study sites across the Czech Republic

The background consists of a hillshade relief layer indicating elevation, where lighter shades represent higher altitudes and darker shades represent lower altitudes (background data source: ČÚZK 2025)

Site list: 1 – Nová Víska, 2 – Litvínov, 3 – Dubí, 4 – Buková Hora, 5 – Růžová hora, 6 – Svor, 7 – Břehyně, 8 – Kryštofovo údolí, 9 – Ferdinandov, 10 – Rakousy, 11 – Rezek, 12 – Janské Lázně, 13 – Zboží, 14 – Chloumek, 15 – Bělečko, 16 – Červenohorské sedlo, 17 – Kochánky, 18 – Štíhlice, 19 – Lhotky, 20 – Chvaletice, 21 – Kouty, 22 – Vápenný Podol, 23 – Krucemburk, 24 – Kuničky, 25 – Konice, 26 – Andělka

measure. A tree was classified as damage-present if it exhibited significant, visible structural impairment, such as peeling bark or the presence of major dead branches. For the 'tree damage' variable, 402 trees were classified as undamaged, and 260 trees showed visible signs of damage. This classification was subsequently used as a categorical predictor in the GLMMs.

Since many stands were mixed-age, determining a precise stand age from planting plans was not feasible. We therefore used tree diameter as a proxy, which is closely correlated with tree age (Černý et al. 1996). Tree diameter was measured at 120 cm above ground level. Canopy closure was evaluated on a three-point scale by visual estimation according to the modified classification from the ICP Forest Expert Panel on Crown Condition and Damage Causes manual (Eichhorn et al. 2020): (1) tree located at the stand edge, (2) tree within a gapped stand, and (3) tree surrounded by neighbouring trees with touching crowns. For the purpose of the GLMMs, this three-point scale was treated as a numeric ordinal variable (ranging from 1 to 3). The total number of sampled trees across these categories was: 82 individuals in category 1 (stand edge), 236 individuals in category 2 (gapped stand), and 344 individuals in category 3 (closed canopy), confirming that all structural positions were sufficiently represented in the analysis.

Climatic variables comprised mean annual temperature and precipitation in 2022, along with spring-specific values reflecting the typical swarming periods of *M. fagi* (April) and *H. annulipes* (May). In addition, we calculated a drought index, expressed as the difference in precipitation between a recent drought period (2015–2019) and a long-term reference period (2005–2009), based on evidence that drought can reduce host tree vitality (Véle, Neudertová-Hellebrandová 2025; Jiang et al. 2022). Precipitation and temperature data were obtained from the Envidata website (Envidata 2024).

Data analysis. To evaluate the factors influencing the abundance of *M. fagi* and *H. annulipes*, two separate generalised linear mixed models (GLMMs) were fitted. Both models used the same set of predictors, with 'site' included as a random effect. Due to overdispersion of the count data, both models assumed a negative binomial distribution with a logarithmic link function. Precipitation in 2022 was excluded from the models due to strong negative collinearity with temperature. Tree diam-

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eter and climatic variables were standardised prior to analysis. All statistical analyses were conducted in R (R Core Team 2020) using the packages 'fitdistrplus' (Delignette-Muller, Dutang 2015) and 'lme4' (Bates et al. 2015, 2024).

RESULTS

Across the 26 different study sites, a total of 5 612 individuals of *Mikiola fagi* were observed, while 853 individuals of *Hartigiola annulipes* were found. *M. fagi* was present at all 26 sites, whereas *H. annulipes* was recorded at 19 of the 26 sites (Table 1). Both the occurrence and abundance of these gall midge species exhibited variability among different study sites (Table 1). The maximum site-level mean proportion of infected leaves was 4.77% for *M. fagi* and 1.96% for *H. annulipes*. The maximum site-level mean number of galls per leaf was 0.56 for *M. fagi* and 0.09 for *H. annulipes*. The absolute maximum number of galls recorded on a single leaf was 12 for *M. fagi* and 15 for *H. annulipes*.

The generalised linear mixed models showed distinct responses of the two gall midge species to tree and climatic variables. The abundance of *M. fagi* was significantly negatively correlated with increasing tree diameter and canopy closure, whereas a positive correlation was found with spring temperature. Other factors (biotic stress, tree damage, mean temperature in 2022, drought index, and spring precipitation) did not show statistically significant effects (Table 2). The abundance of *H. annulipes* was positively correlated with the drought index (Table 3).

Table 1. Mean number of galls per leaf, proportion of infested leaves (%), and maximum number of galls on one leaf recorded at each site

Site	Number of galls/leaf		Proportion of infected leaves (%)		Max. No. of galls	
	M. fagi	*H. annulipes*	*M. fagi*	*H. annulipes*	*M. fagi*	*H. annulipes*
Andělka	0.01	0.01	1.63	0.21	3	8
Bělečko	0.03	0.00	1.08	0.20	3	4
Břehyňský rybník	0.06	0.00	1.60	0.16	4	2
Buková hora	0.28	0.06	3.25	1.36	7	8
Červenohorské sedlo	0.09	0.03	1.72	0.88	7	10
Dubí	0.11	0.01	2.00	0.52	7	2
Ferdinandov	0.28	0.00	3.00	0.04	6	1
Chloumek	0.01	0.01	1.40	0.45	2	6
Chvaletice	0.02	0.00	1.31	0.00	2	0
Janské Lázně	0.08	0.01	1.63	0.42	4	5
Kochánky	0.25	0.09	3.00	1.96	10	12
Konice	0.16	0.05	2.00	1.24	10	6
Kouty	0.03	0.01	1.31	0.23	3	4
Krucemburk	0.05	0.00	1.16	0.20	12	1
Kryštofovo údolí	0.11	0.05	1.74	1.33	6	4
Kuničky	0.56	0.04	4.77	1.13	12	6
Lhotky	0.09	0.04	1.80	0.93	8	12
Litvínov	0.06	0.02	1.38	0.79	7	3
Nová Víska	0.04	0.01	1.36	0.28	5	2
Rakousy	0.17	0.01	2.38	0.27	5	5
Rezek	< 0.01	0.06	0.19	1.19	3	15
Růžová hora	0.09	0.02	2.00	0.67	5	4
Štíhlice	0.19	0.03	2.60	0.57	12	12
Svor	0.23	0.00	2.48	0.08	10	1
Vápenný Podol	0.06	0.00	1.40	0.16	3	3
Zboží	0.03	0.01	0.85	0.38	2	4

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Table 2. Summary of the generalised linear mixed model (GLMM) assessing the influence of biotic and abiotic variables on the abundance of *M. fagi* galls

Predictor	Estimate	SE	*Z*-value	*P*-value
Intercept	2.437	0.221	11.037	< 0.001
Biotic stress	0.247	0.212	1.168	0.243
Canopy closure	–0.316	0.063	–5.026	**< 0.001**
Tree damage	0.069	0.101	0.686	0.492
Diameter	–0.158	0.047	–3.350	**0.001**
Drought index	0.042	0.176	0.237	0.813
Precipitation – spring	0.140	0.287	0.487	0.626
Temperature – average	–0.013	0.254	–0.052	0.958
Temperature – spring	0.513	0.233	2.207	**0.027**

Bold – statistically significant predictors; SE – standard error

Table 3. Summary of the generalised linear mixed model (GLMM) assessing the influence of biotic and abiotic variables on the abundance of *H. annulipes* galls

Predictor	Estimate	SE	*Z*-value	*P*-value
Intercept	0.245	0.409	0.599	0.549
Biotic stress	–0.517	0.541	–0.956	0.339
Canopy closure	–0.210	0.145	–1.446	0.148
Tree damage	–0.208	0.235	–0.885	0.376
Diameter	–0.041	0.118	–0.348	0.728
Drought index	0.477	0.224	2.124	**0.034**
Precipitation – spring	0.692	0.381	1.817	0.069
Temperature – average	0.207	0.323	0.642	0.521
Temperature – spring	0.510	0.318	1.603	0.109

Bold – statistically significant predictors; SE – standard error

DISCUSSION

The preference of *M. fagi* for younger trees, which was indicated by the significant negative correlation between gall abundance and host tree diameter, aligns with the plant defence theory. This theory proposes that resources are allocated differently between defence and growth over the course of a plant's life cycle (Boege, Marquis 2005). Younger trees may allocate more resources to growth at the expense of chemical defences (Neilson et al. 2013; Soderberg et al. 2020), resulting in lower concentrations of quantitative defensive compounds, such as tannins and flavonoids (Price 1991; Barton, Koricheva 2010). Younger trees also tend to host more galls, possibly due to the higher physiological activity of their tissues, which provides a more favourable environment for gall formation. This aligns with the plant vigour hypothesis, which posits that herbivores preferentially feed on the most vigorous parts of their host plants (Price 1991). Thus, the higher gall abundance observed on younger trees is likely a result of both improved physiological suitability and reduced chemical resistance.

The finding that *M. fagi* preferred trees growing in areas with less canopy closure, which is consistent with the findings of Kampichler and Teschner (2002), may be related to the impact of light conditions on leaf quality. The chemical composition of leaves significantly affects host selection by gall-forming organisms (Cornell 1983; Stone et al. 2002). Gall inducers typically seek the best possible balance between defensive secondary metabolite levels and nutritional value (Cornell 1983; White 1993).

Sun-exposed beech leaves exhibit known differences in chemical composition compared to shaded leaves, potentially containing lower concentrations

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of certain defensive compounds (García-Plazaola, Becerril 2001). Consequently, more open canopy conditions could provide *M. fagi* with foliage that is chemically more suitable for gall induction and subsequent larval development. This is significant, as the gall serves both as a physical shelter and a primary nutrient source for the developing larva (Larson, Whitham 1991).

The positive correlation between *M. fagi* abundance and warmer spring temperatures highlights the fundamental role of temperature in driving phenological timing in poikilothermic organisms. Elevated temperatures generally accelerate insect development (Bale et al. 2002). In the case of *M. fagi*, whose primary activity period (encompassing adult emergence, mating, and oviposition) occurs in spring, warmer spring conditions could promote an earlier onset and accelerated completion of these critical life stages (Urban 2000b).

Concurrently, temperature influences host plant phenology, as spring temperatures are a primary driver of budburst timing and leaf development (Fu et al. 2012). Given that *M. fagi* oviposits into nascent, actively developing leaf tissues, precise phenological synchrony with its host tree is essential for successful gall induction (Stone et al. 2002). Elevated spring temperatures lead to an earlier onset of the vegetative period (Menzel et al. 2006; Vitasse et al. 2009). This hypothesis is supported by the observation of higher gall densities on trees exhibiting earlier budburst (Urban 2000b). In contrast, mean annual temperature did not exhibit a significant effect on gall abundance in our study. This finding may be attributed to the ability of intra-gall larvae to tolerate a broad range of external temperatures. This tolerance is likely facilitated by the buffered and relatively stable microclimate within the gall structure, which is characterised by elevated humidity levels (Layne 1991; Wang et al. 2020).

The abundance of *H. annulipes* declined significantly in areas affected by recent drought, suggesting that dry conditions may negatively impact the species' ability to successfully develop on its host. A marginally significant relationship further suggested a negative impact of decreasing spring precipitation. Drought stress is known to alter the physiological state of trees, altering nutrient availability and changing the production of defensive compounds (Da Silva et al. 2011; Seleiman et al. 2021). These changes could make the foliage less suitable for gall induction and larval development. In addition, *H. annulipes* tends to emerge in late spring, a period that often overlaps with the onset of more intense drought stress in temperate forests (Skuhravá, Skuhravý 1974; Hänsel et al. 2019). This timing could further reduce larval survival or success. The relatively high mortality rates observed for this species compared to *M. fagi* (Paclt 1973; Meyer et al. 2020) may reflect this sensitivity to suboptimal conditions.

The study results provide insights for managing young beech stands, particularly as European beech is a key species for forest restoration on clearings after bark beetle calamities (Fuchs et al. 2004; MoA 2024) under changing climatic conditions. The finding that *Mikiola fagi* abundance is positively driven by warmer spring temperatures and lower canopy closure creates a high-risk scenario. Establishing young beech stands on open clearings exposes them to maximum solar radiation and warming. When combined with climate-driven warmer springs, this practice creates ideal conditions for *M. fagi* outbreaks.

We recommend establishing young beech stands under higher canopy closure, for instance, beneath the shading of mature trees. This approach directly informs management under climate change by: (*i*) mitigating the negative effect of low canopy closure identified in our study, and (*ii*) using the shade of mature trees to buffer against the high spring temperatures that favour *M. fagi*. This silvicultural method appears to be a robust adaptation strategy to reduce the susceptibility of young beech stands to secondary pests. Equal emphasis should also be placed on cultivating genetically suitable individuals that are more resistant to stress (Soudek et al. 2024).

CONCLUSION

This study highlighted species-specific responses to environmental and host tree variables. *Mikiola fagi* preferred younger trees in open canopies and benefited from warm springs, whereas *Hartigiola annulipes* was negatively affected by a lack of precipitation (drought). In the context of climate change, *M. fagi* may thus benefit. Establishing young beech stands under higher canopy closure (e.g. under the shading of mature trees) therefore represents a suitable strategy. Nevertheless, this study is subject to certain limitations.

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Notably, single-year data collection, which cannot capture the long-term population dynamics known in gall-forming insects (Urban 2000b; Stone et al. 2002). Furthermore, our analysis omitted soil data (nutrients, water-holding capacity), which can influence host tree defence allocation (Seleiman et al. 2021), and sampling was restricted to the accessible lower canopy (up to 2 m). Future research should prioritise longitudinal monitoring, incorporate detailed soil characteristics, and utilise whole-canopy sampling methods to disentangle the complex interplay of site conditions and climatic drivers.

REFERENCES

Bale J.S., Masters G.J., Hodkinson I.D., Awmack C., Bezemer T.M., Brown V.K., Butterfield J., Buse A., Coulson S.J., Farrar J., Good J.E.G., Harrington R., Hartley S., Jones T.H., Lindroth R.L., Press M.C., Symrnioudis I., Watt A.D., Whittaker J.B. (2002): Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. Global Change Biology, 38: 1–16.

Barton K.E., Koricheva J. (2010): The ontogeny of plant defense and herbivory: Characterizing general patterns using meta-analysis. The American Naturalist, 175: 481–493.

Bates D., Mächler M., Bolker B., Walker S. (2015): Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67: 1–48.

Bates D., Maechler M., Bolker B., Walker S., Christensen R.H.B., Singmann H., Dai B., Scheipl F., Grothendieck G., Green P. (2024): lme4: Linear mixed-effects models using 'Eigen' and S4. R Package Version 1.1-35.

Boege K., Marquis R.J. (2005): Facing herbivory as you grow up: The ontogeny of resistance in plants. Trends in Ecology & Evolution, 20: 441–448.

Călărășanu G., Chira D. (2013): Evolution, biology and control of European beech damaging leaf insects. Revista de Silvicultură și Cinegetică, 18: 112–115.

Černý M., Pařez J., Malík Z.(1996): Růstové a taxační tabulky hlavních dřevin České republiky (smrk, borovice, buk, dub). Jílové u Prahy, IFER: 245. (in Czech)

Černý J., Špulák O., Sýkora P., Novosadová K., Kadlec J., Kománek M. (2024): The significance of European beech in Central Europe in the period of climate change: An overview of current knowledge. Zprávy lesnického výzkumu/Reports of Forestry Research, 69: 74–88.

ČÚZK (2025): Digital Elevation Model of the Czech Republic (DMR 5G). [Dataset] Prague, Czech Office for Surveying, Mapping and Cadastre. Available at: https://geoportal.cuzk.cz (accessed Nov 05, 2025)

Cornell H.V. (1983): The secondary chemistry and complex morphology of galls formed by the Cynipidae (Hymenoptera): Why and how. American Midland Naturalist, 110: 225–234.

Da Silva C.E., Nogueira R.J., Silva M., Albuquerque M. (2011): Drought stress and plant nutrition. Plant Stress, 5: 32–41.

Delignette-Muller M.L., Dutang C. (2015): fitdistrplus: An R package for fitting distributions. Journal of Statistical Software, 64: 1–34.

Eichhorn J., Roskams P., Potočić N., Timmermann V., Ferretti M., Mues V., Szepesi A., Durrant D., Seletković I., Schröck H.W., Nevalainen S., Bussotti F., Garcia P., Wulff S. (2020): Part IV: Visual assessment of crown condition and damaging agents. Version 2020-3. In: UNECE ICP Forests Programme Co-ordinating Centre (ed.): Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Eberswalde, Thünen Institute of Forest Ecosystems: 49. Available at: https://www.icp-forests.org/pdf/manual/2020/ICP_Manual_part04_2020_Crown_version_2020-3_update_06-2023.pdf

ENVIDATA (2024): Online databáze environmentálních dat. Available at: https://www.envidata.cz/ (accessed Dec 12, 2024; in Czech)

Fernandes G.W., Duarte H., Lüttge U. (2003): Hypersensitivity of *Fagus sylvatica* L. against leaf galling insects. Trees – Structure and Function, 17: 407–411.

Ferreira B.G., Moreira G.R.P., Carneiro R.G.S., Isaias R.M.S. (2022): Complex meristematic activity induced by *Eucecidoses minutanus* on *Schinus engleri* turns shoots into galls. American Journal of Botany, 109: 209–225.

Frei E.R., Gossner M.M., Vitasse Y., Queloz V., Dubach V., Gessler A., Ginzler C., Hagedorn F., Meusburger K., Moor M. (2022): European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. Plant Biology, 24: 1132–1145.

Fu Y.H., Campioli M., Deckmyn G., Janssens I.A. (2012): The impact of winter and spring temperatures on temperate tree budburst dates: Results from an experimental climate manipulation. PLoS ONE, 7: e47324.

Fuchs Z., Vacek Z., Vacek S., Cukor J., Šimůnek V., Štefančík I., Brabec P., Králíček I. (2024). European beech (*Fagus sylvatica* L.): A promising candidate for future forest ecosystems in Central Europe amid climate change. Central European Forestry Journal, 70: 62–76.

García-Plazaola J.I., Becerril J.M. (2001): Seasonal changes in photosynthetic pigments and antioxidants in beech (*Fagus sylvatica*) in a Mediterranean climate: Implications for tree decline diagnosis. Australian Journal of Plant Physiology, 28: 225–232.

Gossner M.M., Pašalić E., Lange M., Lange P., Boch S., Hessenmöller D., Müller J., Socher S.A., Fischer M., Schulze E.D., Weisser W.W. (2014): Differential responses of herbivores and herbivory to management in temperate European beech. PLoS ONE, 9: e104876.

Gregoire T.G., Valentine H.T., Furnival G.M. (1995): Sampling methods to estimate foliage and other characteristics of individual trees. Ecology, 76: 1181–1194.

Hänsel S., Ustrnul Z., Łupikasza E., Skalak P. (2019): Assessing seasonal drought variations and trends over Central Europe. Advances in Water Resources, 127: 53–75.

Jactel H., Petit J., Desprez-Loustau M.L., Delzon S., Piou D., Battisti A., Koricheva J. (2012): Drought effects on damage by forest insects and pathogens: a meta-analysis. Global Change Biology, 18: 267–276.

Jiang Y., Marchand W., Rydval M., Matula R., Janda P., Thom D., Fruleux A., Buechling A., Pavlin J., Nogueira J., Dušátko M., Málek J., Kníř T., Veber A., Svoboda M. (2024): Drought resistance of major tree species in the Czech Republic. Agricultural and Forest Meteorology, 348: 109933.

Kampichler C., Teschner M. (2002): The spatial distribution of leaf galls of *Mikiola fagi* (Diptera: Cecidomyiidae) and *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae) in the canopy of a Central European mixed forest. European Journal of Entomology, 99: 79–84.

Knížek M., Liška J., Véle A. (2023): Occurrence and importance of the bark beetles of the genus *Pityokteines* in silver fir (*Abies alba*) stands. Zprávy lesnického výzkumu/Reports of Forestry Research, 68: 168–175. (in Czech)

Langer G.J., Bußkamp J. (2023): Vitality loss of beech: A serious threat to *Fagus sylvatica* in Germany in the context of global warming. Journal of Plant Diseases and Protection, 130: 1101–1115.

Larson K.C., Whitham T.G. (1991): Manipulation of food resources by a gall-forming aphid: The physiology of sink-source interactions. Oecologia, 88: 15–21.

Layne J.R. (1991): Microclimate variability and the eurythermic nature of goldenrod gall fly (*Eurosta solidaginis*) larvae (Diptera: Tephritidae). Canadian Journal of Zoology, 69: 614–617.

Lee H., Romero J. (2023): Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, IPCC: 42.

Lorenc F. (2023): Ophiostomatoid fungi on Scots pine (*Pinus sylvestris* L.) stands affected by long-term drought. Zprávy lesnického výzkumu/Reports of Forestry Research, 68: 28–36. (in Czech)

Machar I., Vlčková V., Buček A., Voženílek V., Šálek L., Jeřábková L. (2017): Modelling of climate conditions in forest vegetation zones as a support tool for forest management strategy in European beech dominated forests. Forests, 8: 82.

Menzel A., Sparks T.H., Estrella N., Koch E., Aasa A., Ahas R., Alm-Kübler K., Bissolli P., Braslavská O., Briede A., Chmielewski F.M., Crepinsek Z., Curnel Y., Dahl Å., Defila C., Donnelly A., Filella I., Jatczak K., Måge F., Mestre A., Nordli Ø., Peñuelas J., Pirinen P., Postolache C., Roetzer A., Rusticcini M., Scheifinger H., Schlünzen K.H., Stojnic S., Toth Z., Trnka M., Wittich K., Zust A. (2006): European phenological response to climate change matches the warming pattern. Global Change Biology, 12: 1969–1976.

Meyer S., Rusterholz H.P., Baur B. (2020): Urbanisation and forest size affect the infestation rates of plant-galling arthropods and damage by herbivorous insects. European Journal of Entomology, 117: 34–48.

MoA (2024): Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2023. Prague, Ministry of Agriculture of the Czech Republic: 128. Available at: https://nli.gov.cz/wp-content/uploads/zprava-o-stavu-lesa-a-lesniho-hospodarstvi-ceske-republiky-v-roce-2023.pdf (in Czech)

Molnár B.P., Boddum T., Hill S.R., Hansson B.S., Hillbur Y., Birgersson G. (2018): Ecological and phylogenetic relationships shape the peripheral olfactory systems of highly specialized gall midges (Cecidomyiidae). Frontiers in Physiology, 9: 883.

Neilson E.H., Goodger J.Q.D., Woodrow I.E., Møller B.L. (2013): Plant chemical defense: At what cost? Trends in Plant Science, 18: 250–258.

Paclt J. (1973): Preliminary studies on the susceptibility of *Fagus sylvatica* to gall-forming insects. Centralblatt für das gesamte Forstwesen, 90: 186–192.

Pilichowski S., Giertych M.J. (2020): Two galling insects (*Hartigiola annulipes* and *Mikiola fagi*), one host plant (*Fagus sylvatica*) – Differences between leaf and gall chemical composition. Baltic Forestry, 26: 474.

Price P.W. (1991): The plant vigor hypothesis and herbivore attack. Oikos, 62: 244–251.

R Core Team (2020): R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. Available at: http://www.R-project.org

Prudic K.L., Oliver J.C., Bowers M.D. (2005): Soil nutrient effects on oviposition preference, larval performance, and chemical defense of a specialist insect herbivore. Oecologia, 143: 578–587.

Rouault G., Candau J.N., Lieutier F., Nageleisen L.M., Martin J.C., Warzée N. (2006): Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science, 63: 613–624.

Ryall K.L., Fidgen J.G., Turgeon J.J. (2011): Detectability of the emerald ash borer (Coleoptera: Buprestidae) in asymptomatic urban trees by using branch samples. Environmental Entomology, 40: 679–688.

https://doi.org/10.17221/64/2025-JFS

Seleiman M.F., Al-Suhaibani N., Ali N., Akmal M., Alotaibi M., Refay Y., Dindaroglu T., Abdul-Wajid H.H., Battaglia M.L. (2021): Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants, 10: 259.

Skrzypczyńska M. (2008): Masowy pojaw hartigiolówki bukowej *Hartigiola annulipes* (Hartig) (Diptera: Cecidomyiidae) na liściach buka zwyczajnego *Fagus sylvatica* L. w Ojcowskim Parku Narodowym. Sylwan, 152: 26–29. (in Polish)

Skuhravá M., Roques A. (2000): Palaearctic dipteran forest pests. In: Papp L., Darvas B. (eds): Contributions to a Manual of Palaearctic Diptera. Vol. 1. General and Applied Dipterology. Budapest, Science Herald: 651–692.

Skuhravá M., Skuhravý V. (1974): Gall midges (Diptera, Cecidomyiidae) on forest trees and shrubs in E. Slovakia. Lesnictví, 20: 159–165. (in Czech)

Skuhravá M., Skuhravý V., Meyer H. (2014): Gall midges (Diptera: Cecidomyiidae: Cecidomyiinae) of Germany. Faunistisch-Ökologische Mitteilungen, Supplement 38: 1–100.

Soderberg D.N., Bentz B.J., Runyon J.B., Hood S.M., Mock K.E. (2020): Chemical defense strategies, induction timing, growth, and trade-offs in *Pinus aristata* and *Pinus flexilis*. Tree Physiology, 40: 1196–1210.

Soudek P., Podlipná R., Langhansová L., Moťková K., Dvořáková M., Petrová Š., Haisel D., Satarova T.M., Dobrev P.I., Gaudinová A., Máchová P., Véle A., Fulín M., Cvrčková H., Hošek P., Berchová-Bímová K. (2024): Stress responses to bark beetle infestations among pine (*Pinus sylvestris*), fir (*Abies alba*), and beech (*Fagus sylvatica*) trees. Forests, 15: 1761.

Stone G.N., Schönrogge K., Atkinson R.J., Bellido D., Pujade-Villar J. (2002): The population biology of oak gall wasps (Hymenoptera: Cynipidae). Annual Review of Entomology, 47: 633–668.

Urban J. (2000a): Bionomy and polymorphism of galls of the beech leaf gall midge (*Mikiola fagi* Htg.) (Diptera, Cecidomyiidae). Journal of Forest Science, 46: 114–126.

Urban J. (2000b): Vliv doby rašení buku lesního (*Fagus sylvatica* L.) na vývoj larev a tvorbu hálek bejlomorky bukové (*Mikiola fagi* Htg.). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, 48: 97–117. (in Czech)

Véle A., Neudertová Hellebrandová K. (2025): Drought is the primary driver of *Sirex noctilio* outbreaks in Czechia. Zprávy lesnického výzkumu/Reports of Forestry Research, 70: 85–92. (in Czech)

Vitasse Y., Porté A.J., Kremer A., Michalet R., Delzon S. (2009): Responses of canopy duration to temperature changes in four temperate tree species: Relative contributions of spring and autumn leaf phenology. Oecologia, 161: 187–198.

Walter J.A., Ives A.R., Tooker J.F., Johnson D.M. (2018): Life history and habitat explain variation among insect pest populations subject to global change. Ecosphere, 9: e02274.

Wang C., Liu P., Chen X., Liu J., Lu Q., Shao S., Yang Z., Chen H., King-Jones K. (2020): Microenvironmental analysis of two alternating hosts and their impact on the ecological adaptation of the horned sumac gall aphid *Schlechtendalia chinensis* (Hemiptera, Pemphiginae). Scientific Reports, 10: 435.

White T.C.R. (1993): The Inadequate Environment: Nitrogen and the Abundance of Animals. Berlin, Springer Science & Business Media: 425.

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