

Habitat preference of *Daphne laureola* L. (Thymelaeaceae) at its north-eastern range margin

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Received: 2024.05.23.; Revised: 2025.10.16.; Accepted: 2025.10.18.

Key words: actual vegetation, altitudinal distribution, dolomite, forests, potential vegetation, Vértes Mountains.

Abstract: Spurge-laurel (*Daphne laureola* L.) reaches the north-eastern limit of its range in the Vértes Mountains (Central Hungary). In Europe, it inhabits various plant communities, including beech woodlands. In Hungary, its primary habitat is beech woodlands, and it is the characteristic species of the Transdanubian Mountains beech forest (*Daphno laureolae-Fagetum*) association. In this study, the species' habitat preference in the Vértes Mountains was examined based on 2635 occurrences and 725 vegetation stands. We searched for associations between *D. laureola* occurrences and actual and potential vegetation, the degree of naturalness of habitats, and elevation. It was found that the occurrence of *D. laureola* is restricted to certain vegetation types in the Vértes Mountains. Considering the actual vegetation, the plant can be found in beech woodlands, sessile oak-hornbeam woodlands, sessile oak-Turkey oak woodlands, downy oak woodlands, and occasionally in tree plantations, shrublands and grasslands. *D. laureola* was found to be positively associated with beech woodlands, sessile oak-hornbeam woodlands, sessile oak-Turkey oak woodlands, and downy oak woodlands, while negatively associated with non-natural vegetation types and grasslands. As to the potential vegetation, the positive association of *D. laureola* occurrences is valid for beech woodlands and downy oak woodlands, but not for sessile oak-Turkey oak woodlands and sessile oak-hornbeam woodlands. Based on the degree of naturalness of habitats, 87% of the species' occurrences fall into the natural or the near-natural categories. *D. laureola* occurs in the Vértes Mountains between 350 and 450 m altitude most frequently, while in a considerable part of its range in Europe, it is a montane species appearing in 500–1500 m elevation. Such altitudinal distribution in the Vértes Mountains is similar to that of several coexisting herbaceous relict montane species living on dolomite rocks or in rock grasslands there. However, unlike those, *D. laureola* prefers forest habitats. Based on these, *D. laureola* can be considered a good, natural indicator species of undisturbed original forest stands in the Vértes Mountains. Furthermore, the presence of *D. laureola* supports the phytogeographical connection of the dolomite areas in the Vértes Mountains to the montane flora of higher altitudes in Europe.

Citation: Barina Z., Csontos P. 2025: Habitat preference of *Daphne laureola* L. (Thymelaeaceae) at its north-eastern range margin. Bot. Közlem. 112(2): 225–236.
<https://doi.org/10.17716/BotKozlem.2025.112.2.225>

Introduction

The evergreen shrub *Daphne laureola* L. (Thymelaeaceae) is distributed around the Mediterranean, including the Atlantic-Mediterranean areas, where it extends northwards as far as Scotland. Beyond the Mediterranean area, it occurs in the north-east direction as far as Hungary, Slovakia and Austria. It is an infrequent and protected species all over its native range (FUKAREK 1962, PRUGGER 1973, DIMOVA and VLADIMIROV 2006, OPREA et al. 2010), albeit it is an invasive shrub in Denmark and Sweden (POWO 2025), and in the western parts of Canada and the US (LEI 2014, STRELAU et al. 2018), on the southern coast of Crimea (BAGRIKOVA et al. 2021) and at some localities in the Southern Hemisphere (BAKER 2013). The available phytocoenological records are incomplete and contradictory. *D. laureola* is regarded primarily as a species of beech woodlands over most of its distribution area (MATTANOVICH 1972, PRUGGER 1973, PIGNATTI 1982, SOČO et al. 2002, FISCHER et al. 2005, OPREA et al. 2010), although records from xerotherm woodlands are also known from various parts of its range (ŠUGAR and TRINAJSTIĆ 1970, BLEČIĆ 1972, KELLER 1999). In Hungary, the species has a remarkably narrow distribution in the central part of the country, restricted to the Bakony and Vértes Mountains, and a locality near the town of Keszthely, altogether covering an area of about 1500 km² (KELLER and TIBORCZ 2012). Several subsynchronous occurrences of *D. laureola* are also known to the northeast of this area (e.g. HASZONITS et al. 2021). According to current knowledge, in this territory, the species almost exclusively appears in beech woodlands or in associated rocky or ravine woodlands (SOÓ 1966, SIMON 2000, BARTHA 2009), albeit there are also observations in xerothermic oak woodlands (KELLER 1999). *D. laureola* is a characteristic species of the *Daphno laureolae-Fagetum* beech forest association specific to the region (BORHIDI and SÁNTA 1999, BORHIDI et al. 2012).

Daphne laureola was first reported from the Vértes Mountains (Central Hungary) in 1914 (LÁNG 1914), and later it was found to be not rare but scattered in the region (KELLER 1999), and missing from the surrounding areas (BARINA 2006). Prompted by the remarkable occurrence of *D. laureola* in the Vértes Mountains at the north-eastern margin of its distribution range, we aimed to identify the species' habitats and explore its possible preferences there.

Material and methods

The Vértes Mountains is roughly 30 km long and comprises Triassic dolomite. Its area is 314 km², the highest point is 487 m a.s.l. The annual mean tem-

perature in the area is 9–10 °C, the precipitation varies between 600–700 mm per year, with an annual maximum in May (BIHARI et al. 2018).

Our field surveys to collect distribution records for *D. laureola* were conducted between 2002 and 2014. Geographical coordinates of solitary individuals or clones were recorded by Garmin eTrex Legend GPS (2002–2005), Garmin eTrex Venture Cx (2006–2007), Garmin eTrex Legend HCx (2008–2012) and Garmin Montana 680t (2013–2014) GPS devices. The vegetation of the study area was mapped between 2005 and 2011, when field surveys were assisted by aerial photographs and the above GPS records. Habitat types (categories of actual vegetation) followed BÖLÖNI et al. (2011). Each habitat was classified according to the Németh–Seregélyes five-grade scale of habitat naturalness (MOLNÁR et al. 2007) as well, and the types of potential vegetation were identified following ZÓLYOMI (1967). All maps (*D. laureola* occurrences, actual vegetation, potential vegetation, habitat naturalness, elevation) were edited by using the Quantum GIS (QGIS 2.6.1) software and the same program was used for spatial queries and statistical analyses. The association between the occurrence of *D. laureola* and the actual vegetation, potential vegetation, degree of naturalness or elevation was investigated by using the Yule association coefficient (ZAR 2010). Some *D. laureola* occurrences fell outside the area covered during vegetation mapping. These data were not considered in the vegetation type versus occurrence location analysis but were included in other calculations. The asymmetry of altitudinal distribution was tested by calculating its skewness (YULE and KENDALL 1950).

Results

Altogether 2635 occurrences of *D. laureola* were encountered in the area studied (Fig. 1). These were from 725 vegetation stands, overwhelmingly from forest communities with only 13 records from grassland habitats. Some vegetation stands surveyed contained multiple *D. laureola* occurrences, and there were 201 *D. laureola* records in localities where the vegetation was not mapped. The forest communities with *D. laureola* included beech woodlands (K5), sessile oak-hornbeam woodlands (K2) and oak woodlands (L1, L2a) with 278, 735 and 1184 records, respectively. 156 occurrences are from rocky woodlands (K5) and 67 are from scrublands and plantations (L3, P1, P2b, R1, R2, S1, S4, S5; Table 1).

D. laureola appeared in 20–30% of the stands of each oak (L1, L2a), sessile oak-hornbeam (K2) and beech (K5) woodlands reaching a maximum of 31% in beech woodlands. The highest value (50%) was observed for scattered trees

or narrow tree lines of non-native species (S7), but this can't be evaluated since data are not representative (only two stands were encountered out of which one contained *D. laureola*) (Table 1). Based on the area of habitat patches, more than 60% of the sessile oak-hornbeam woodlands (K2) and that of rocky woodlands (K6) host *D. laureola*, this value is more than 50% for thermophilous oak woodlands (L1) and around 40% for Turkey oak woodlands (L2a) and for beech woodlands (K5). A negative association was found between the occurrence of *D. laureola* and each grassland and almost all non-natural communities

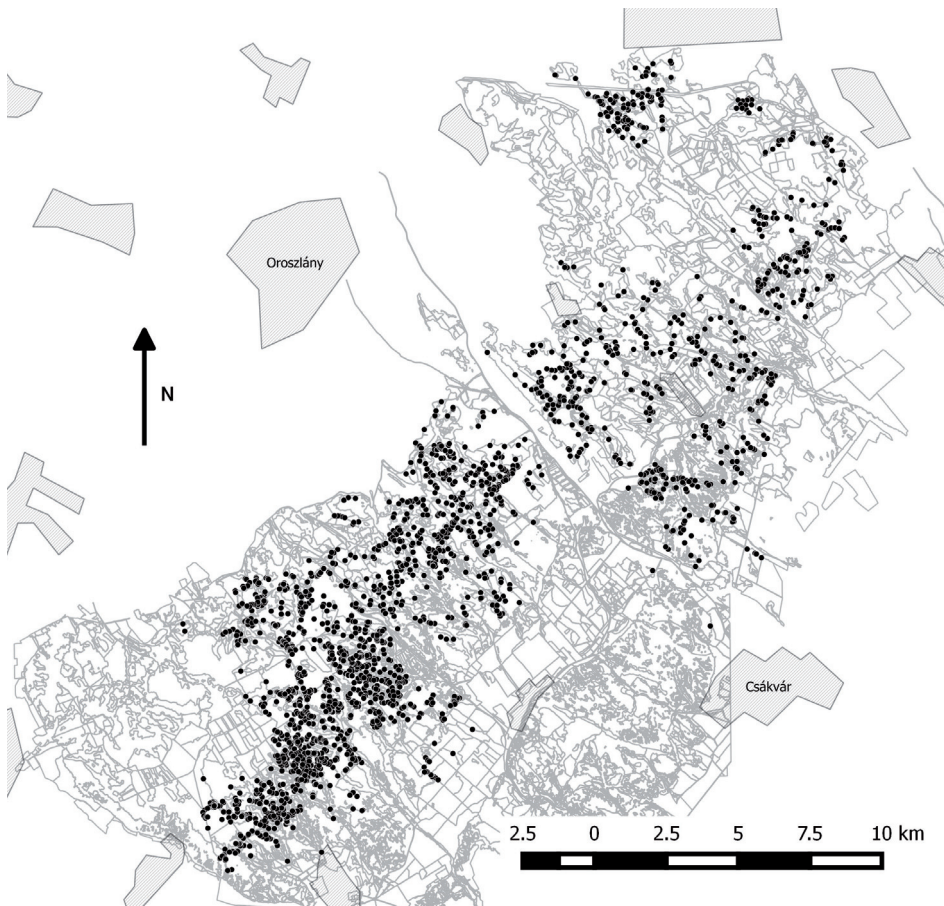


Fig. 1. Distribution of *Daphne laureola* in the Vértes Mountains, Hungary. Black dots indicate *D. laureola* occurrences, the pattern of gray lines in the background shows the boundaries of the stands for the different habitat types.

1. ábra. A babérboroszlán (*Daphne laureola*) előfordulásai a Vértesben (fekete pontok). A háttér szürke vonalakkból álló mintázata a különböző élőhelyek állományainak határait jelöli.

Table 1. Number of *Daphne laureola* occurrences in Á-NÉR habitat types (actual vegetation categories) and the species' association to the habitat types in the Vértes Mountains.**1. táblázat.** A *Daphne laureola* előfordulások száma élőhelytípusonként, és a faj asszociáltságának mértéke az egyes élőhelytípusokhoz a Vértesben.

Á-NÉR code	Habitat type	Number of stands with <i>D. laureola</i>	Yule association coefficient
E1	<i>Arrhenatherum</i> hay meadows	1	-0.86
H1	Closed rocky grasslands	1	-0.89
H3a	Slope steppes on stony soils	3	-0.85
H4	Semi-dry grasslands, woodland-steppe meadows	8	-0.93
K2	Sessile oak-hornbeam woodlands	735	0.66
K5	Beech woodlands	278	0.70
K6	Rocky woodlands	156	0.51
L1	Closed thermophilous <i>Quercus pubescens</i> woodlands	544	0.65
L2a	Pannonian-Balcanic – <i>Quercus cerris</i> - <i>Quercus petraea</i> woodland	640	0.60
L3	Xerotherm, relict rocky woodlands	1	0.33
P1	Saplings of native tree species	24	0.16
P2b	Dry shrub vegetation	7	-0.79
R1	Spontaneously afforested areas	1	0.18
R2	Mixed woodlands with native and non-native tree species	15	0.53
S1	<i>Robinia pseudoacacia</i> plantations	1	-0.58
S4	Scots and black pine plantations	17	-0.36
S5	Plantations of other conifers	1	-0.41
S7	Scattered trees or narrow tree lines of non-natives tree species	1	0.85

(E1, H1, H3a, H4, S1, S4, S5; Table 1). The high positive association with S7 is ignored due to the non-representative sample. Semi-natural communities (P1, R1) show a slight positive association with the presence of *D. laureola*, while all natural woodland habitats (K2, K5, K6, L1, L2a, L3) show a strong positive association with *D. laureola* occurrence. The degree of naturalness is 5 or 4 in 63.3% and 23.7% of the habitat patches containing *D. laureola*, respectively, i.e. 87% of the surveyed patches are natural habitats. Habitat patches ranked as degraded (values 1 to 3) are recently cut woodlands or aged plantations of non-native tree species.

As to the potential vegetation of the area, the presence of *Daphne laureola* showed a strong positive association with the distribution of beech woodland and thermophilous woodland, while a negative association with the distribution

of Turkey oak woodland and sessile oak-hornbeam woodland (Fig. 2). In the Vértes Mountains, *D. laureola* is missing from the north-western and south-eastern foothills, where sessile oak-hornbeam and Turkey oak woodlands dominate.

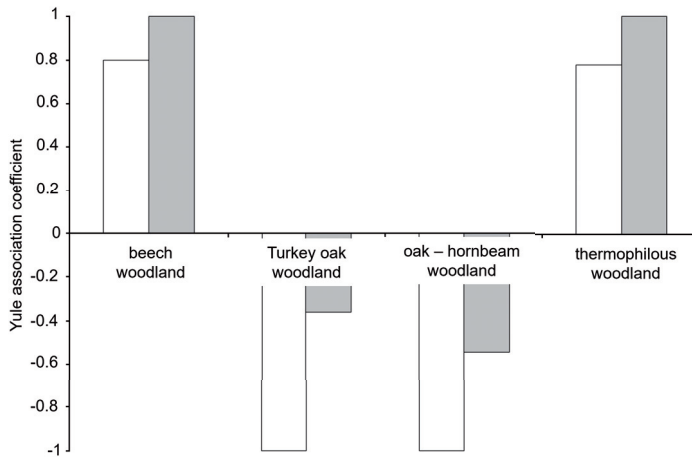


Fig. 2. Correlation between the occurrence of *Daphne laureola* in the Vértes Mountains and potential vegetation types according to the Yule association coefficient calculated with stand area (empty bars) and stand number (filled bars) of vegetation types.

2. ábra. A *Daphne laureola* Vértes hegységi előfordulásainak korrelációja a potenciális vegetációtípusokkal a Yule asszociációs koefficiens alapján az egyes vegetációtípusok területrészesedése (üres oszlopok), valamint az állományaik száma (kitöltött oszlopok) figyelembevételével.

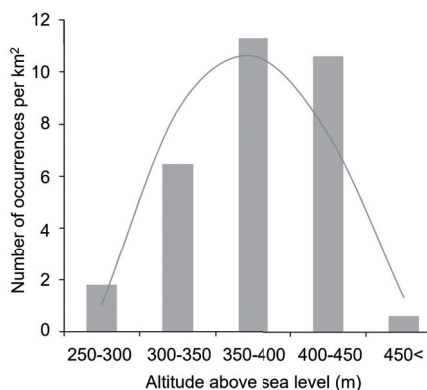


Fig. 3. Frequency of *Daphne laureola* according to elevation intervals in the Vértes Mountains (columns). To better visualize the shape of the distribution, an extrapolated Gaussian curve is fitted to the data (continuous line).

3. ábra. A *Daphne laureola* előfordulási gyakorisága magassági intervallumok szerint a Vértesben (oszlopok). A diagramra rárajzoltuk az adatokból számított Gauss-görbét (folytonos vonal), hogy az eloszlás alakja jobban kivehető legyen.

Daphne laureola is distributed altitudinally between 190 and 470 m a.s.l. in the study area with very few occurrences below 250 m. The frequency of *D. laureola* is the highest in the altitude 350–400 m, somewhat lower between 400–450 m, and much less below 300 m and above 450 m (Fig. 3). The skewness of the frequency distribution according to altitude is -0.4173 , indicating a longer tail below the most preferred elevation zone (as areas above 450 m are very restricted in the study area). The species strongly prefers elevations between 350–450 m (Fig. 3).

Discussion

Despite reaching the north-eastern margin of its distribution, *D. laureola* is a frequent plant in the Vértes Mountains but missing from the surrounding territories. This is in line with the observation of ZÓLYOMI (1942) that Central Hungary is a transitional biogeographical zone where the range of several species terminates, and some of them attain a high abundance in this marginal situation in spite of that they are already on the edge of their area. *Fraxinus ornus* L., a tree of southern Europe reaching its northern limit of distribution in the Carpathian Basin, is another good example for this phenomenon by expressing high morphological plasticity and wide habitat tolerance in northern Hungary (CSONTOS et al. 2001, KALÁPOS and CSONTOS 2003). Our result also corresponds to the findings of CASTILLA et al. (2011, 2012), who reported no significant differences in the density and genetic diversity of populations in central and marginal populations of *D. laureola*, presumably because of the presence of large populations on the local margins. At the north-eastern margin of its native area, *D. laureola* occurs in various forest communities, and occasionally also in open habitats. Rarely it appears in tree plantations and survives in forest clearcuts. In the Vértes Mountains, the characteristic habitats of *D. laureola* are natural woodlands, which cannot be considered as ‘ancient’ woodlands as was found by ROSE (1999) in England.

Daphne laureola – considered as a characteristic species of the *Daphno laureolae-Fagetum* association – is frequent in beech-dominated stands in the Vértes Mountains. However, it equally prefers oak and oak-hornbeam dominated communities; while is missing from the entire area of the neighbouring Gerecse Mountains to the north, although the mentioned woodland communities have extended stands there (BARINA 2006). Regarding the potential vegetation, *D. laureola* prefers beech and thermophilous oak woodlands. This apparently dual preference can be explained by the remarkable loss of the areas of Turkey oak and oak-hornbeam woodlands and the destruction or transformation of their stands.

Daphne laureola is the most frequent at the elevation zone between 350 and 400 m, while does not prefer areas above 450 m or below 250 m. In the latter zone, in oak-hornbeam or beech forests, *D. laureola* was present in only one (KEVEY and RIEZING 2023) or three (KEVEY et al. 2021) of the 25 sampled locations. Over most of its native range, *D. laureola* is a montane species (CASTILLA et al. 2011); however, it is a lowland species in Great Britain (KELLER 1999) and grows in 50–650 m elevation in Crimea, where it is an alien plant (BAGRIKOVA et al. 2021). Its presence in the Vértes Mountains is similar to the isolated appearance of a number of montane taxa, even widely distributed in low altitudes in Central Hungary far from their nearest occurrences in the Alps and the Carpathians. These species are restricted to open dolomite habitats (*Draba lasiocarpa* Rochel, *Phyteuma orbiculare* L., *Daphne cneorum* L.) or rock woodlands (*Primula auricula* L., *Carduus glaucus* Baumg., *Aquilegia vulgaris* L.) in this area. Their presence is the consequence of the specific characters of the dolomite bedrock (ZÓLYOMI 1942). Other, predominantly montane taxa (*Dryopteris expansa* (C. Presl) Fraser-Jenk., *Crepis paludosa* (L.) Moench, *Cardamine amara* L.) are also characteristic in this region and are confined to riverine alder woodlands on sandy soil in the Vértes Mountains (BOROS 1954), again in altitudes under 350 m above sea level. Based on these data, *D. laureola* is descending from mountain areas and inhabits various mesophilous and xero-mesophilous woodlands in the same area.

Due to the preference of inner, least disturbed areas of the Vértes Mountains, and stands with original plant communities, *D. laureola* can be regarded a good indicator of natural woodland habitats with outstanding natural conservation value.

Acknowledgements

The authors would like to thank Csaba Németh (Institute of Ecology and Botany, HUN-REN Centre for Ecology) for the chorological records of the studied species and Gabriella Somogyi for checking the draft of the manuscript. The journal editors also improved the manuscript with many useful comments and suggestions, for which the authors are particularly grateful.

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A babérboroszlán (*Daphne laureola* L., Thymelaeaceae) élőhely-preferenciája elterjedési területének északkeleti határán

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Érkezett: 2024.05.23.; Átdolgozva: 2025.10.16.; Elfogadva: 2025.10.18.

Kulcsszavak: aktuális vegetáció, dolomit, erdőtársulások, magassági elterjedés, potenciális vegetáció, Vértes.

Összefoglalás: A babérboroszlán (*Daphne laureola* L.) Magyarországon, a Vértes területén éri el elterjedésének északkeleti határát. Elterjedési területén különböző növénytársulásokból, gyakran bükkösökből jelzik, míg hazánkban kimondottan bükkös fajként ismert és a dunántúli-középhegységi bükkösök (*Daphno laureolae-Fagetum*) karakterfaja. A faj élőhely-preferenciáját a Vértes területén gyűjtött 2635 előfordulási pont és 725 vegetációfolt adatai alapján elemeztük. Az előfordulásokat többféle jellemző szerint vetettük össze a hegység élőhelytérképével: aktuális és potenciális vegetáció, természetesség, tengerszint feletti magasság. Megállapítottuk, hogy a babérboroszlán elterjedése a Vértes területén belül is bizonyos vegetációtípusokra korlátozódik. Az aktuális vegetációt tekintve, a növény megtalálható bükkösökben, gyertyános- és cseres-tölgyesekben, valamint molyhos tölgyesekben; esetenként ültetvényekben, cserjésekben és gyepekben is megjelenik. Míg a bükkösök, gyertyános- és cseres-tölgyesek, valamint molyhos tölgyesek elterjedése és a *D. laureola* előfordulásai között pozitív kapcsolat mutatkozik, a nem természetes élőhelyek és gypálmányok elterjedésével negatív a kapcsolat. A potenciális vegetációt tekintve a pozitív kapcsolat már csak a bükkösökre és molyhos tölgyesekre igaz, míg a cseres- és gyertyános-tölgyesek esetében ez nem jelentkezik. A faj előfordulásainak 87%-a természetvédelmi értékszámként is a természetes, illetve természetközeli kategóriába esik. A babérboroszlán európai elterjedési területének jelentős részén hegyvidéki élőhelyeken, 500–1500 m közötti magasságban jelenik meg, a Vértes területén azonban 350–450 m között fordul elő leginkább, hasonlóan a dolomitsziklákon, sziklagyepekben megjelenő hegyvidéki reliktfajokhoz, azoktól eltérően azonban erdei élőhelyeken. Mindezek alapján a babérboroszlán eredeti

erdőállományok jó, természetes jelzőfajának tekinthető a Vértesben széles élőhely-preferenciával, és a hegység dolomitterületeinek hegyvidéki kapcsolatait támasztja alá.

Idézés: Barina Z., Csontos P. 2025: Habitat preference of *Daphne laureola* L. (Thymelaeaceae) at its north-eastern range margin. Bot. Közlem. 112(2): 225–236.
<https://doi.org/10.17716/BotKozlem.2025.112.2.225>