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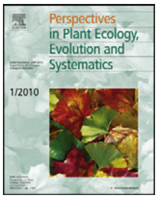

Biological flora of Central Europe

Biological flora of Central Europe: *Ceratocapnos claviculata* (L.) Lidén

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ABSTRACT

The eu-oceanic therophytic woodland herb *Ceratocapnos claviculata* has been expanding north- and eastwards into north temperate and subcontinental regions during the past decades. The rapid range expansion of the species may be an example of a species which is strongly profiting from global change. Against this background, in the present paper we review the taxonomy, morphology, distribution, habitat requirements, life cycle and biology of the species.

Introduction

The annual forest herb *Ceratocapnos claviculata* has been regarded an eu-oceanic species due to its distribution pattern in W Europe(Jäger and Werner, 2005). However, during the last decades the species showed both an increase in frequency within its range (Buttler, 1986; Decocq, 2000; Hill et al., 2004; Van der Eerden et al., 1998; Voss et al., 2011) and a rapid range expansion east- and northwards into sub-oceanic and northern-temperate regions (Benkert et al., 1995; Oredsson, 2005). Several ideas have been put forward as explanations for the recent spread of *C. claviculata*. These are closely related to the sequence of factors and filters that determine the invasibility of a local community (Lortie et al., 2004; Davis et al., 2005). (1) Seed dispersal: anthropogenic activities, such as transport of wood and forest management (seed transport through machinery) may be responsible for the fast regional expansion and local spread, respectively (Benkert et al., 1995; Buttler, 1986; Decocq, 2000; Horstmann, 2005; Lethmate et al., 2002; Oredsson, 2005). (2) Increased winter temperatures: after seeds have been dispersed to a new locality, mild winter temperatures (as a consequence of e.g. climate change) may facilitate seedling survival and the establishment of populations (Lethmate et al., 2002; Folland and Karl, 2001). (3) Soil eutrophication: increased atmospheric nitrogen inputs may increase the performance of this species after successful establishment (Pott and Hüppe, 1991; Vannerom et al., 1994; Van der Eerden et al., 1998). Thus, its ongoing range expansion may be another example of a "footprint of climate change" (e.g. Walther et al., 2005).

In order to gain deeper understanding of factors governing the range expansion of *C. claviculata*, it appears appropriate to summarize the available information on the biology of *C. claviculata* in a comprehensive review.

The taxonomy and nomenclature follows Wisskirchen and Haeupler (1998).

Taxonomy and morphology

Taxonomy

C. claviculata (L.) Lidén, Anal. Jard. Bot. Madrid 41: 221. 1984. – Rankender Lerchensporn – Climbing Corydalis, (greek κέραζ = horn, due to the horned fruits, the word component *capno-* comes from the Greek καπνοζ = smoke referring to the similarity with fumewort (Fumaria) from Latin *fumus* "smoke". *Clavicula* is Latin for tendril or twine).

Homotypic synonyms: *Fumaria claviculata* L. Species Plantarum: 701, 1753, *Corydalis claviculata* (L.) De Candolle, Flore française: 638, 1805, *Capnodes claviculata* (L.) Kuntze, Revisio Generum

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Plantarum 1: 14, 1891, *Capnoides claviculata* (L.) Druce, Fl. Berkshire: 36, 1897, *Pseudofumaria claviculata* (L.) Büscher & G.H. Loos, Veröff. Bochumer Bot. Ver.: 14, 2010.

Heterotypic synonyms: no heterotypic synonyms seem to exist.

C. claviculata belongs to the family Fumariaceae DC., subfamily Fumarioideae (DC.) Endlicher, which sometimes is assigned family level (Stevens, 2001). Until 1986 (Lidén, 1986) it was assigned to the genus *Corydalis* section *Stylotome* Prantl. Like most species of the section, *C. claviculata* is characterized by fibrous roots, sympodial growth, yellowish flowers, many seeded fruits and a deciduous style which is sharply set off from the ovary. In contrast, the closely related tribe *Fumarieae* Rchb. has only one-seeded fruits and an indeciduous style (Fedde, 1960). However, it differs from the majority of the *Corydalis* species by developing tendrils and having two cotyledons instead of just one (Fedde, 1960).

Lidén (1986) relocated the whole section *Stylotome* to the Mediterranean centered tribe *Fumarieae*. Despite the objections above, the transfer may be justified by the sharing of, e.g. a caducous, chlorophyll-less style, chromosome length, sympodial shoot structure and zygomorphic flowers in bracteolate racemes. Consequently, the species is assigned to the subtribe *Sarcocapninae* Lidén and the genus *Ceratocapnos* Dur.

The genus *Ceratocapnos* is recognized by ribbed fruits, filiform hairs and stigma characters (Lidén, 1986). Particularly stigma structure is considered taxonomically useful for characterization of tribe, section and genus (e.g. Ryberg, 1960; Brückner, 1984; Lidén, 1986).

The genus comprises only three species, all of them being annual and scandent due to tendrils. While *C. claviculata* is mainly distributed in temperate W Europe (Fig. 1), the other two species, *Ceratocapnos heterocarpa* Dur. and *C. turbinata* (DC.) Lidén are confined to the western and eastern Mediterranean region, respectively. Despite the historical changes of the generic name and uncertainty of higher taxonomic placement, there was never any taxonomic confusion concerning the identity of the species.

Despite the lack of fibrous clusters in the pericarp, ribs and hairs, the transfer of the species from *Corydalis* to *Ceratocapnos* as a monophyletic group was supported by Fukuhara and Lidén (1995a), who claim that the asymmetrical stigma and the spongy endocarp could be considered an autapomorphy *C. claviculata* shares with the other

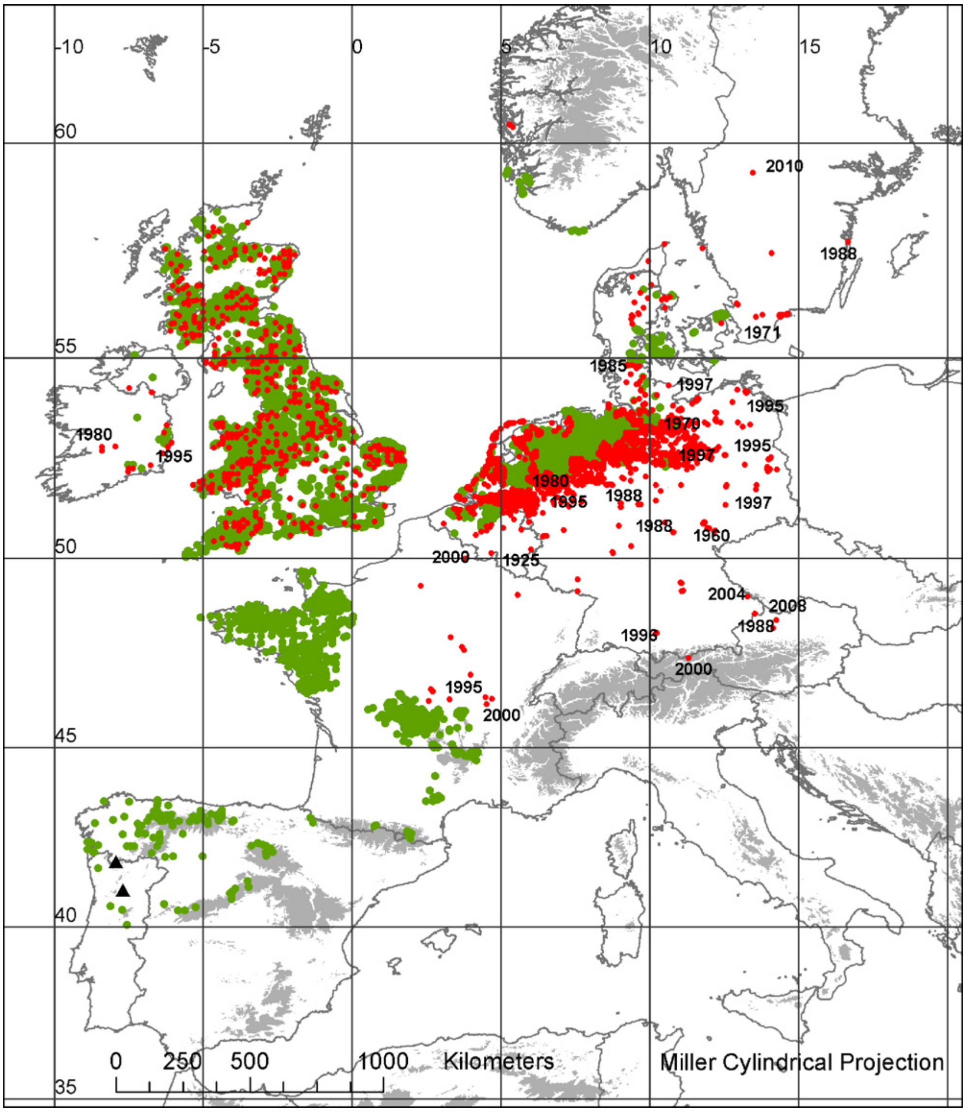

Fig. 1. Geographical distribution of *Ceratocapnos claviculata*. Distribution data were compiled by E. Welk from floristic literature and databases. Records until 1930 are denoted by green dots; records between 1930 and 2010 by red dots. Occurrences of the subspecies *Ceratocapnos claviculata* ssp. *picta* are marked with triangles. For some of the recent records the date of first record is given. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

two species of the genus. However, owing to many similarities between the genera *Pseudofumaria* and *Ceratocapnos* and using a relatively wide definition of genera, Loos (2010) proposed to combine these two genera, retaining the older name *Pseudofumaria* as genus name (see also above, homotypic synonyms).

From the surroundings of Vila Nova de Paiva, province Beira Alta, Portugal, the infraspecific taxon *picta* has been described as a variety by Sampaio (1935). Castroviejo (1998) stated that it could not be recollected again and assigned it to subspecies level (*C. claviculata* subsp. *picta* (Samp.) Lidén). However, there seem to be recent occurrences reported from the Parque Nacional da Peneda-Gerês, province Trás-os-Montes and Alto Douro, N Portugal (Vicente, 2005), as well as from Parque Natural Baixa Limia Serra Xurés, province Galicia, Spain (Rodríguez and Pereira, 2008; Fig. 1). It is very similar to the subsp. *claviculata* but differs in having rose flowers and puberulous capsules due to the presence of small vesicular hairs (Castroviejo, 1998). Interestingly, *C. heterocarpa* Dur. and *Ceratocapnos turbinata* (DC.) Lidén also have rose-red petals.

Morphology

Habit: *C. claviculata* is a herbaceous, slender, hemirosette, climbing plant species. Due to the weakly developed supporting tissue, the more or less branched, four-angular stem is very weak but can reach up to 200 cm length (mean = 42.4 cm, Table 1, see also chapter "Life cycle").

Shoot system: The shoot system of *C. claviculata* is characterized by sympodial growth (Buchenau, 1861; Buttler, 1986; Fig. 2). The primary shoot bears five to ten leaves before the apical meristem is terminated by an inflorescence, which is situated in a lateral position in 180° opposition to a leaf. Long before flowering, the uppermost axillary bud continues the mother shoot in direction of the main axis by pushing aside the last raceme; it also terminates after two nodes (α and β prophyll) with an inflorescence. This monochasial branching pattern is repeated for several shoots and eventually finishes when environmental conditions become unfavorable. Lower buds that have not taken part in the formation of shoots, i.e. the bud in the first node of the side shoot and in the primary axis in the buds occurring in each of the axils may later grow out as lateral shoots (Ryberg, 1960). In *C. claviculata*, buds were found even in the axils of the cotyledons, but only in one case in the greenhouse under optimum conditions those buds could be observed forming shoots (Buttler, 1986).

Roots: The species forms only a sparsely branched shallow root system which is rooting in the humus layer under natural conditions (Lethmate et al., 2002; Voss et al., unpublished). As an annual plant, *C. claviculata* develops no belowground storage organs. The very fibrous primary roots show low cambial growth activity, which soon ceases completely (Ryberg, 1960).

Leaves: The leaves are spirally organized along the stem and rarely pseudo-opposite. They are long petiolate and once or twice pinnate with alternate long leaflets composed of a few entire, elliptic-obovate, tapering segments. These leaflets have three nerves. The number of leaflets increases with length of the shoot. At a stage when the plant comprises two to five leaves, owing to very short internodes, these leaves still grow rosette-like (hemirosette) (Fig. 3). Afterwards, elongation of the stem increases and the internodes can reach up to 5 cm length. The laminae of the segments become smaller in the upper leaves. At the end of the rachis the one to two outer pinnate pairs of leaflets and the final pinnae, petioles and petiolules may strongly elongate and transform into branched tendrils (Fig. 3). Often the transformed lamina of the leaflets is still visible as small distal hooks (Goebel, 1928; Ryberg, 1955; Buttler, 1986).

Table 1

Plant traits of *Ceratocapnos claviculata*. Individuals and seeds were collected in the field in 2008. For germination, seeds were exposed for two months to a temperature of 4 °C in Petri dishes in a climate chamber. Means and standard errors (±s.e.) for the regions NW Spain (NW-E, 6 populations), The Netherlands (NL, 17 populations), NW Germany (NW-G, 19 populations), S Sweden (S-S, 20 populations), NE Germany (NE-G, 18 populations) and for the entire range. ANOVA results with *F* statistic (*F*), degrees of freedom (df), *p*-value (*p*) and sample size (*n*) are shown for each measured variable. Superscripted letters indicate significant groups (HSD test). Regions are arranged according to increasing continentality.

	NW-E		NL		NW-G		S-S		NE-G		Range					
	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.	*F*	df	*p*	*n*
Dry mass, above ground (g)	–	–	0.91^{b}	0.29	1.87^{b}	0.46	0.77^{b}	0.15	0.2^{a}	0.03	0.95	0.14	28.02	3	<0.001	378
Shoot length (cm)	–	–	50.1^{c}	2.72	43.9^{b}	3.34	44.7^{cb}	2.89	29.7^{a}	1.91	42.4	1.45	3.420	3	0.022	377
SLA (m^2 kg^{-1})	–	–	50.88^{ab}	5.03	57.96^{ab}	3.53	44.15^{b}	3.76	63.99^{a}	7.07	53.3	2.57	2.765	3	0.048	74
Inflorescences/individual	–	–	28.8^{c}	7.0	28.7^{bc}	6.3	16.5^{b}	2.4	8.6^{a}	1.0	20.8	2.5	4.910	3	0.002	378
Flowers/inflorescence	8.3^{c}	0.2	7.0^{b}	0.1	6.2^{a}	0.1	7.9^{c}	0.1	5.6^{a}	0.1	6.9	0.1	55.45	4	<0.001	1383
Seeds/capsule	2.32^{c}	0.07	2.02^{b}	0.03	2^{b}	0.04	2.1b^{c}	0.04	1.9^{a}	0.04	2	0.02	9.840	4	<0.001	1090
Mass 1000 seeds (g)	1.114^{c}	0.024	1.124^{a}	0.012	1.238^{a}	0.014	1.329^{b}	0.009	1.321^{b}	0.009	1.263	0.007	18.96	4	<0.001	198
Germination (%)	21.2^{a}	3.8	53.8^{b}	2.8	71.2^{c}	2.2	55.2^{b}	4.8	46.0^{b}	5.9	54.3	2.3	11.92	4	<0.001	82
Ovules/flower	2.1	0.2	2.3	0.1	2.4	0.1	2.1	0.1	2.3	0.1	2.2	0.1	1.312	4	0.268	162
Pollen/flower	412.9^{a}	29.2	151.3^{a}	20.2	509.1^{a}	48.3	512.3^{a}	15.0	413.6^{a}	46.5	488.9	13.0	2.853	4	0.026	162
PO-ratio	232.7	37.0	238.7	14.2	226.7	26.4	259.3	13.1	195.4	25.3	236.2	8.6	1.628	4	0.170	162

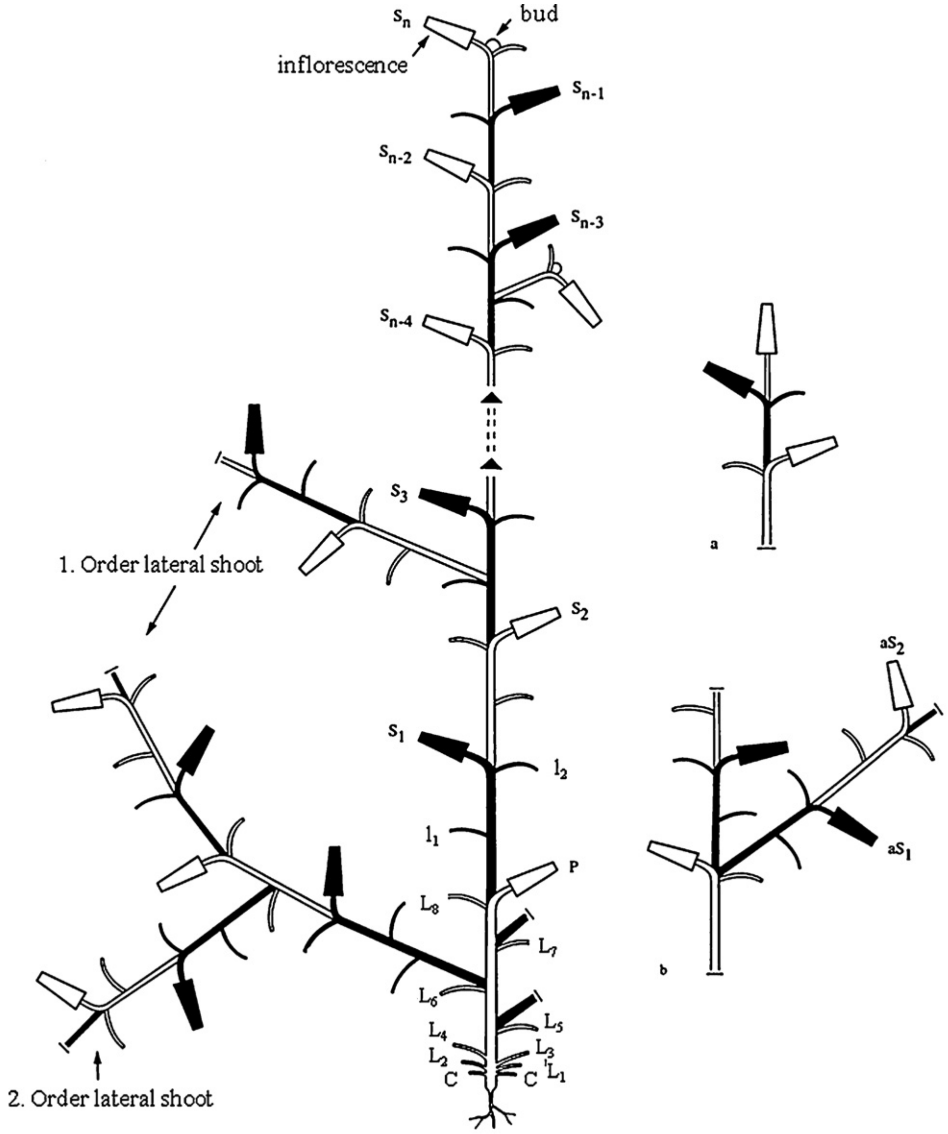

Fig. 2. Diagram of the sympodial shoot system (Buttler, 1986). For easier identification, consecutive shoots inclusive of their leaves alternate in black and white. The leading shoot consists of the consecutive primary shoot (=P) and the lateral shoots (=S_1-S_n) forming a shoot sequence: P–S_1–S_2–. . .–S_{n-1}–S_n. The structure of the first and second order lateral shoots is equal to that of the leading shoot. Leaves of the primary shoot are labeled L_1–L_8, those of the first lateral shoot are labeled l_1 and l_2. C = cotyledons, trapeze = inflorescence, circle = bud. Occasionally there are exceptions to this structure: (a) a sequence may directly end with a bud, (b) additional buds occur, which may develop into accessory lateral shoots aS_1, aS_2, etc.

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Juvenile *C. claviculata* exhibits only ordinary, unmodified leaves. However, in adult plants any intermediate stage between tendrils and usual leaves can be found. Thus, in the upper region of the plant most of leaves end as tendrils while basal leaves often lack tendrils completely (Ryberg, 1960).

The development of tendrils begins in the distal parts of the juvenile rachis, which becomes thinner and longer. The tendrils possess a mechanical sensitivity. If a tendril comes into contact with an object, which serves as mechanical stimulus, it forms a spiral coil in such a direction as to envelope the object, coils around and thus becomes anchored (Darwin, 1867; Jaffe and Galston, 1968).

The species cannot grow upright by itself unless it attaches to elevated supports during elongation. However, if nothing appropriate can be found, no free coiling occurs and the tip of the tendril bends downwards and inwards and loses its haptotrophic sensibility and power of movement. Thus, only juvenile tissue is able to elongate and coil. The sensitivity decreases stepwise from the tip towards the base of the lamina. The internodes are not sensitive (Darwin, 1867).

Inflorescences: In *C. claviculata* the flowers are arranged in simple, bracteous, open (polytelic) racemes. The main shoot is terminated by a polytelic raceme and the following partial inflorescences are organized as a monochasial thyrsoidal synflorescence that sometimes is supported by basal paracladia (lateral shoot systems that repeats the structure of the main synflorescence). According to Ryberg (1960) the number of flowers of a single raceme can range between one and thirteen but lies mostly between 6 and 10. We observed inflorescences ranging from a minimum of 1 to a maximum of 20 flowers but 50% of the samples had 5–8 flowers (mean = 6.9 ± 0.1, n = 1383, Table 1, see also chapter “Life cycle”). The racemes are long pedunculate, often with small, tender hairs at the base of the peduncle. The cream-coloured flowers are 5–6 mm long (Lidén, 1986; Ryberg, 1955; Fig. 3). Schultze-Motel (1986) states that flowers might reach a

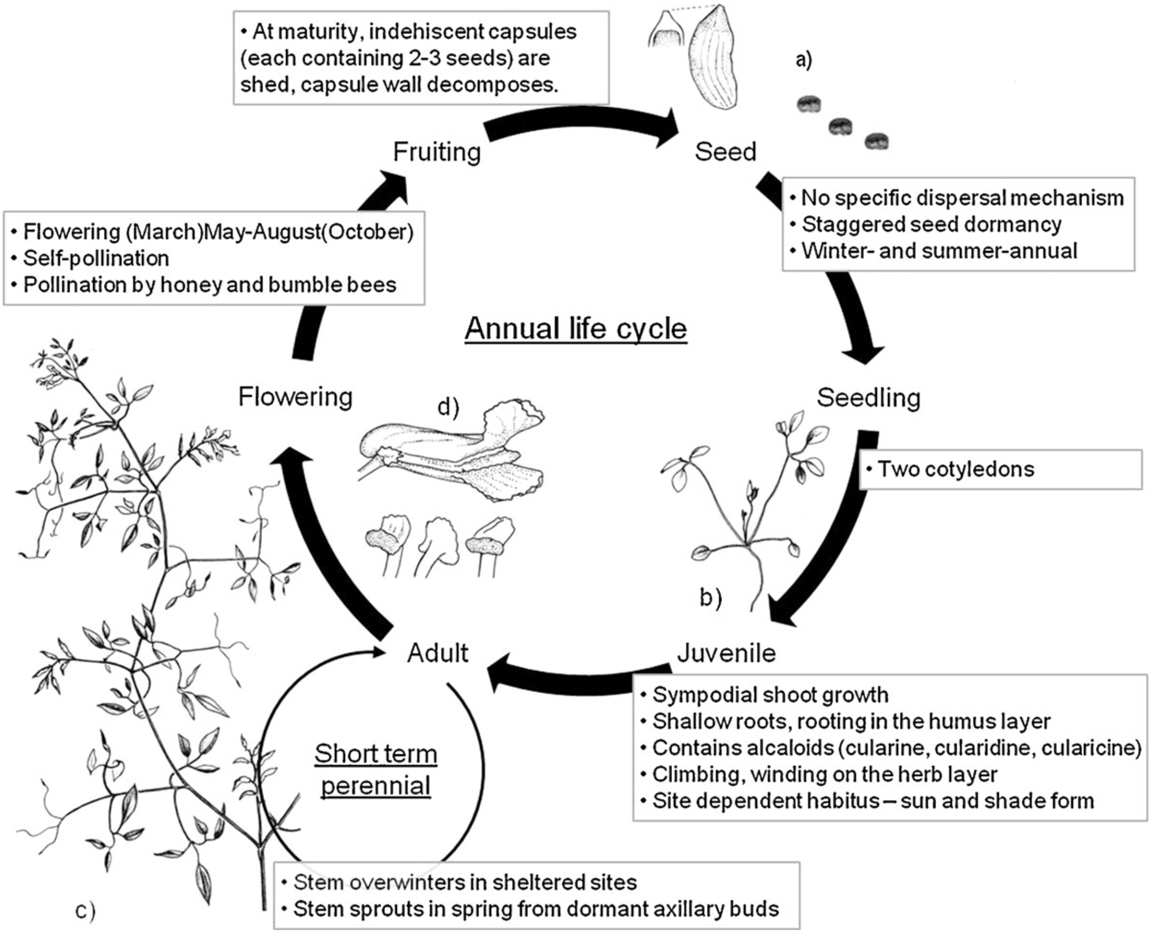

Fig. 3. Life cycle of *Ceratocapnos claviculata*. (a) Mature fruit with horned beak and seeds (Lidén, 1993). (b) Approximately 6 week old juvenile plant with two cotyledons (Buttler, 1986). (c) Flowering adult plant with tendrils (Buttler, 1986). (d) Flower and stigma from different perspectives (Buttler, 1986; Lidén, 1993).
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maximum length of 10 mm but we have never observed flowers of that size. As in *Corydalis* the racemes are bracteolate. At the base of the very short pedicels of each flower there is a small, about 1 mm long, lanceolate bract which is very similar to the scale-like, lapsed sepals (Lidén, 1986).

Flower: *C. claviculata* has transverse-zygomorphic flowers. The flower consists of four petals in two whorls. The inner, oblong petals are coherent at the tip, jointed about the middle and have well developed median wings. They are dark purple spotted internally, which is not visible from the outside. Internal mottling is found in most taxa in Fumariaceae, but so far, a function is not known. The inner petals are enclosing the androecium and the gynoecium. The outer petals are winged at the apex. The outer, upper petal carries a saccate, downwards curved spur (Ryberg, 1955). The spur seems to be on the lower side but in fact originally it was situated sidewards and changed its position during development due to torsion of the pedicel by 90° (Fedde, 1960).

Gynoecium: In Papaveraceae (inclusive Fumariaceae) exist homo- (fruit opens sutural) and heterocarpellate (fruit opens bivalvate) gynoecia. The gynoecia in Fumariaceae are heterocarpellate since the two carpellae are morphologically not identical. *C. claviculata* has a free superior ovary. It contains 1–4 ovules which are all developing into seeds. The fruit is a capsule with parietal–marginal placentation (Brückner, 1984). The style, which is translucent and chlorophyll-free, is sharply set off from the ovary and is separated from it by a distinct incision. A light touch suffices at the end of the flowering season to separate it from the ovary (Ryberg, 1960). The stigma consists of a large membranous, oblique dentate crest and an oblong, lateral fleshy structure presumably equivalent to papilla tissue. Except of *C. heterocarpa* no other species within the Fumariaceae has a similar stigma (Ryberg, 1960; Fig. 3).

Androecium: The androecium consists of six anthers carrying eight thecae. There are two stamen bundles, each with one central dithecal and two lateral monothecal anthers. The anthers are rounded-elliptic, closely adhering to the stigma on which the pollen is deposited. So, self fertilization may occur frequently and is supported by the pollen/ovule ratio of the species (see chapter “Reproduction”). However, Hart (1874) observed that at the time of maturity the stigma projects slightly so that it would be first touched by the proboscis of an insect. Furthermore, he suggests that it may be slightly protogynous. The stamen and the petals are connate at the base. In the subtribe *Sarcocapninae* the upper stamen is stouter than the lower and filaments are hyaline. Almost all species of the subtribe *Sarcocapninae* are characterized by pantocolpate pollen with linear-elliptic, often faint, colpi (Lidén, 1986). The generalized flower morphology is described by the floral formula K2 C2 + 2 A (1/2+1 + 1/2) + (1/2 + 1 + 1/2) G2 (Bresinsky et al., 2008). At the base of the stamen there is nectariferous tissue. In all *Fumarieae* these nectaries are prolonged and may reach far into the spur. The nectaries are supplied by the central vascular bundle and are partly fused with the spur of the outer petal. Even autogamous species produce nectar, except in depauperate or cleistogamous flowers (Lidén, 1986, 1993).

Seeds: The seeds are dorsal–apical laterally flattened, smooth and shiny black. With a length of 1.5–2 mm they are relatively large in relation to the size of flowers and fruits (Fukuhara, 1999). The seeds are anacampylotropic due to a curved micropyle–hilum–chalaza axis.

The species has a small and flat aril which joins broadly at the hilar region. It is tonguelike, white, fleshy, composed of enlarged cells and reaches to the center of the seed (Fukuhara, 1999). However, Cappers et al. (2006) does not mention an aril for *C. claviculata* and Ryberg (1955) mentions only a "very inconspicuous" arilloid. Neither in the closely related subtribe Sarcocapninae (except genus *Pseudofumaria*) nor in the other two taxa of the genus *Ceratocapnos* an aril has been described (Lidén, 1986).

Seed coat anatomy: In general seed-coat anatomy is very informative for systematics at the tribal, generic and species levels and thus has been described in detail for Fumarioideae (Brückner, 1985; Fukuhara and Lidén, 1995b; Fukuhara, 1999). *Ceratocapnos* belongs, together with some Corydaleae genera and two other Fumarieae genera (*Cysticapnos* and *Pseudofumaria*), to the same seed-coat type. However, taxa belonging to the same seed-coat type are not monophyletic, thus the similar anatomy might be a result of parallel evolution (Fukuhara and Lidén, 1995b). The cells of the exotesta are wholly filled with dark deposits serving in most Fumarioideae as protective tissue.

Embryology: At the time of dispersal the seed consists mainly of endosperm while the embryo is still very small and little differentiated. It matures during the following weeks (Buchenau, 1861). In Fumarioideae seeds have a multi-layered nucellus (crassinucellate) which contains the embryo sac (Fukuhara and Lidén, 1995b). The embryo sac is monosporic (Lidén, 1993). In *Corydalis* and *Pseudofumaria* the embryo consists of only two cells at the time of seed shedding and its maturation requires low temperatures (Lidén, 1993). Since also in *C. claviculata* cold stratification increased germination to a large extent (see chapter "Germination"), immaturity of the embryo may represent morphological dormancy.

Fruit: Fruit characters have often been used for subdivision in Fumarioideae (e.g. Fedde, 1960; Lidén, 1986; Brückner, 1992; Fukuhara and Lidén, 1995a). *C. claviculata* develops silicular, glabrous, approximately 1 cm long capsules, which are narrowing towards the apex and thus forming a beak (Fedde, 1960). This sterile beak is part of the ovary and not of the style (Ryberg, 1960). In respect to the pericarp, in Fumarioideae four squarely arranged vascular bundles enter the fruit base; they include two valve-central bundles and two replum bundles. In *Sarcocapnos* and *C. heterocarpa*, clusters of fibres along the valves form longitudinal ribs on the fruit, which are missing in *C. claviculata*.

The endocarp of the fruits envelops the ripe seeds and sometimes separates from the outer part. In the genus *Ceratocapnos* the endocarp and the innermost layer of the mesocarp are detached together. In *C. claviculata* this applies only for the apical part of the fruits (Fukuhara and Lidén, 1995a). In most taxa, the cells of the endocarp are isodiametric and have strongly undulated boundaries. In *Ceratocapnos* this is more pronounced than in other genera, so that the convex parts of the outline protrude like branches and the cells are loosely arranged making the endocarp rather spongy (Fukuhara and Lidén, 1995a). The exocarp is thin-walled. In *C. claviculata* also the mesocarp is mainly composed of thin-walled parenchymatic cells. Vascular bundles are distributed in the middle of the parenchyma or near the endocarp. In contrast to other species of *Fumarieae*, *C. claviculata* lacks longitudinal fibres along the vascular bundles and in the mesocarp (not either in *Pseudofumaria*) and clusters of sclerenchyma. However, it has latitudinal fibres that accompany the bundles at the base of the fruit appendage, which explains the indehiscence of the fruits that also occurs in other taxa of *Sarcocapnineae* (Fukuhara and Lidén, 1995a). (For the number of seeds see chapter "Life cycle".)

Distribution and habitat requirements

Geographical distribution

C. claviculata is an eu-oceanic species native to W Europe. The geographical distribution ranges from N Portugal in the Southwest to N Scotland in the Northwest, S Norway in the North and from easternmost Denmark in the Northeast to S France in the Southeast (Fig. 1). The species is reported to be native from the following European countries: Portugal, Spain, France, Ireland, United Kingdom, Belgium, Netherlands, Germany, Denmark, and Norway. Non-native occurrences are reported from Sweden (Oredsson, 2005) and, quite recently, from Austria (Kleesadl, 2009). The highest densities of *C. claviculata* populations are reported from Great Britain, W France, Belgium, The Netherlands, and NW Germany. Thus, the European atlantic floristic province of Takhtajan (1986) represents the current range center of the species, and the general distribution can be described as submeridional to temperate within the continentality regions 1–2 in Europe. The respective range formula after Jäger and Werner (2005) reads sm/mo-temp c1-2 EUR.

In the Temperate floristic zone, the species occurs from the planar to the colline altitudinal zone, yet is predominantly confined to lowlands (Fig. 4, 80% of occurrences between ca. 0 m and 300 m asl.) In the submeridional floristic zone, extending northwards to approximately 46° N in W Europe, a clear shift towards montane habitats is visible (Figs. 1 and 4). This sharp altitudinal shift is enforced by the geographical disjunction between the lowland occurrences in NW France and the occurrences in the Massif Central. Additionally, there is a higher amount of altitudinal variation visible in this range part, since, e.g. in Spain, the species grows in the lowlands of coastal, air-humid Galicia from 80 to 120 m (Castroviejo, 1975) but also in the Picos de Europa from 1200 to 1500 m (Rivas-Martínez et al., 1984) and in the Sierra de Guadarrama at altitudes of up to 1750 m (Fernández-González, 1991), probably because in the interior territories air-humid climates are confined to higher altitudes.

Several other plant species share a similar general distribution pattern and are therefore classified as a range type or floristic element. Meusel et al. (1965) assign *C. claviculata* to the *Ulex* range type. This type contains species of atlantic heathlands, acidic mires and woodlands that are completely or mostly confined to the atlantic floristic province. The name giving species *Ulex europaeus* is similar to *C. claviculata* amongst the Oceanic Temperate species as it has also spread from its native range eastwards into Europe, and now has a Suboceanic Temperate distribution. Further species with similar distribution are *Wahlenbergia hederacea* (L.) Rchb., *Lobelia urens* L., *Cirsium anglicum* D.C., *Sedum anglicum* Huds., *Scilla verna* L., or *Hypericum helodes* L. Thorough studies of this plant distribution range type have been provided by Dupont (1962) and Roisin (1969). The climatic features were summarized by Gimingham (1972) and can be best described as cool temperate conditions with high rainfall and low annual temperature oscillation. Species of this range type seem to avoid both, areas with low air humidity in the vegetation period and very low winter temperatures and thus are mostly absent from mediterranean and continental areas. In a recent ecogeographical analysis of the European atlantic heathlands (Loidi et al., 2010) ordinations showed that the main climatic factors determining heathland floristic distribution are thermicity (thermicity index; $[[T+M+m]\times 10]$, T: yearly average temperature, M: average maximum temperature of the coldest month of the

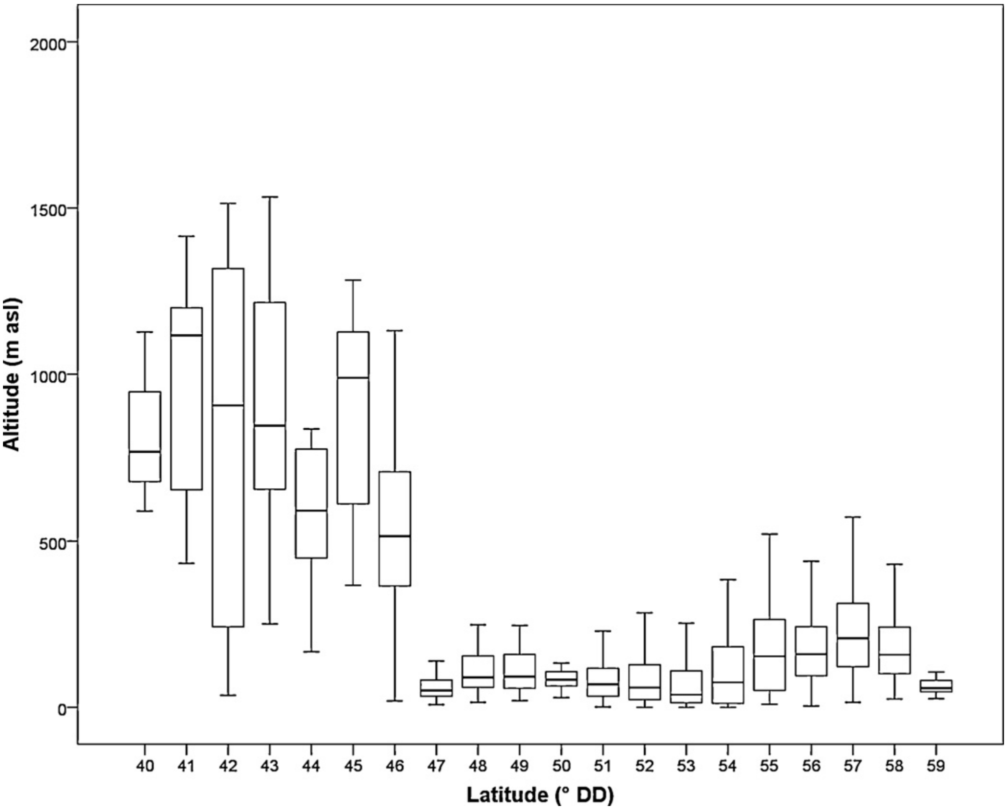

Fig. 4. Box and whisker plots of the altitudinal distribution of *Ceratocapnos claviculata* along latitude classes of one degree. Data are extracted from the compiled distribution data. Indicated are the lower and upper quartiles (box), the median (bold line), as well as the 1.5× interquartil range (whiskers), outliers mostly based on data resolution issues are removed.

year, *m*: average minimum temperature of the coldest month of the year) and summer drought (potential evapotranspiration for the 3 summer months).

Given the supposed frost sensitivity and the relatively high demands on humidity, the question arises where *C. claviculata* might have persisted during the Quaternary glacials, especially the Last Glacial Maximum. Nearly all phylogeographic studies for Europe focused on species that are supposedly far more cold resistant than *C. claviculata*. Mahy et al. (1999) report that *Calluna vulgaris* might have survived in two regions during the last glaciation events: SW Europe and S Britain. For *C. claviculata*, only the supposed SW Iberian pleistocene refugium for temperate species might be regarded as suitable. The re-colonization of W Europe probably might have originated from refugia considerably south of the species' current distribution range. Migrants from this refugium were the likely source of colonists for populations occupying the previously or meanwhile unsuitable lowland habitats along the NE atlantic coasts. Since all the above hypotheses remain highly speculative, phylogeographic investigations using molecular markers are urgently needed for a better understanding of both, the distributional history and future of the species.

Habitat

Regarding light requirements, in the indicator value evaluation of Ellenberg et al. (1992) the species obtained a light value of 5 and thus mainly prefers semi-shaded sites. Indeed, most populations occur in semi-shaded open oak-, birch-, and pine-forests, in fringes, hedgerows or ditches along roads. However, the species also thrives very successfully on sun exposed forest clearings (Buchenau, 1861; Tüxen and Jahns, 1962; Buttler, 1986; Fukarek and Henker, 2006).

On the other hand, in the UK *C. claviculata* grows in mixed woodland with a canopy cover of at least 20% (Hill et al., 2004). However, in dark beech forests, unfavorable light conditions seem to prevent the colonization by *C. claviculata* and in the course of succession from open to more shady habitats the species usually declines (e.g. Pollmann and Lethmate, 2006; Voss et al., 2011; but see Benkert et al., 1995).

The preferential occurrence in half-shady locations is also in line with the species' water requirements: in Central Europe, *C. claviculata* usually occurs on fresh soils of intermediate moisture (Lethmate et al., 2002). Also in the southwestern part of its range, in N Spain and SW France, the species grows in forests and hedges on fresh soils but it may also be found on walls and more or less shady, rocky sites with an inclination of 0–10% (Castroviejo, 1998; Dupont, 2001). In this kind of habitat, humus accumulating crevices may favor therophytic pioneers like *C. claviculata* but the shallow soil layer may become very dry during summer (Clement and Touffet, 1977). The occurrence of the species on sun exposed sites and rocky slopes contrasts with its slender, hygromorphic habit and its poorly developed, little-branched root system, predominantly rooting in the surface layer. However, low water storing capacity of these habitats may be compensated by low evapotranspiration rates due to the atlantic climate with high air humidity through mist or high amounts of precipitation during the time of germination (autumn–spring) and growth (spring–early summer). The annual precipitation e.g. in the atlantic zone of N Spain is between 900 and 1800 mm with a mean annual temperature of 5 °C in the subalpine and 9.3 °C in the montane zone (Rivas-Martínez et al., 1984). One of the southernmost occurrences of the species lies in the Sierra de Guadarrama in Spain. Here, *C. claviculata* is found only in a few north-exposed mountainous beech forests. Soils in these habitats have a good water supply due to annual precipitation sums of between 1000 and 1400 mm and an annual mean temperature of only 6–10 °C (Fernández-González, 1991). In the native range, the lowest long term mean values of annual precipitation of about 540–550 mm are to be found at occurrences in the East-Anglia counties of SE England. The driest regions within the broadened synanthropic range are the sub-oceanic regions Saxony-Anhalt and Saxony (E Germany) where the species is found in forests and degenerated bogs (Rattey, 1984; Kühn and Gutte, 1997), and in SE Sweden (Kalmar county), where long term means of 500–530 mm precipitation are calculated (SMHI, 2006; DWD, 2010).

Obviously, the lower values for precipitation and temperature are quite similar between the native and the recently invaded range. Indeed, when testing monthly mean values for precipitation and temperature and bioclimatic variables (Hijmans et al., 2005), isothermality and MTWQ (mean temperature of the wettest quarter) were the only variables that differed between native and non-native occurrences to a larger degree. Both variables are connected with changes from oceanic to suboceanic–subcontinental climate. Towards the East and away from the atlantic and North Sea coasts the temperature differences between summer and winter increase, as well as the proportion of summer rain at the annual precipitation sum (Welk, unpubl.).

C. claviculata is mostly growing on humic, acidic and moderately acidic soils of intermediate to high fertility (Ellenberg et al., 1992; Hill et al., 2004). The species roots in the organic surface layer, which consists mostly of moder or raw humus, or of hardly decomposed litter formed by needles, and leaves of trees or grasses (Passarge and Hofmann, 1968; Decocq, 2000; Lethmate et al., 2002; Horstmann, 2005). The thickness of this layer may range from about 1 to 30 cm (Voss et al., unpublished data).

In The Netherlands, Germany, Belgium, Sweden and the UK, the subsequent mineral soil often is dominated by a sandy to silty fraction of low fertility. Across the species' range various types of bedrock can be found such as quartz sand, sandstone, granite, gneiss, crystalline or schistous rocks. The soil types developing on these substrates range from acid brown soils to podzols and to pseudo- and stagnogleys (Tüxen and Diemont, 1937; Rodwell, 1998). The shallow soils on rocky slopes of quartzite and schist in France and Spain are mostly developed as ranker (Provost, 1993; Castroviejo, 1998; Dupont, 2001). Typically all soils mentioned above have a low base status and are acidic with pH values from less than 3.5 to 4.6 (Clement et al., 1980; Rodwell, 1998; Dengler et al., 2007; Voss et al., unpublished data). In general, the species is absent from limestone areas unless it is overlain by non-calcareous substrate as described by Horstmann (2005) for the occurrence of the species on calcareous silty loam, which was covered by 20–25 cm of raw humus so that the lime did not affect the shallow-rooted herbal layer.

This preference for acidic soils seems to be one of the main reasons for the disjunct distribution of the species in France. Here, the northern range part is sharply limited by Cretaceous and Jurassic parent materials surrounding the Paris basin. A comparison of the distribution pattern with geological maps indicates that *C. claviculata* is confined to islands of geologically acidic parent materials of Cambrian and Pre-Cambrian age (Hercynian domain). A lower frequency of occurrence is also recognizable for the Jurassic region in England. Following from this geologically constraints, the Vosges region in easternmost France might potentially provide geologically suitable habitats for the species. Interestingly, acidic soil types of different parent material that occur abundantly in regions like Haute-Normandie, Centre (Loire, Loire-et-Cher, Cher), and Aquitaine (Gironde, Landes), are not populated by the species (Welk, unpubl.).

C. claviculata typically occurs on leached, oligotrophic soils (e.g. Passarge and Hofmann, 1968; Rattey, 1984). However, during the last 50 years nitrogen availability in soils increased as a consequence of atmospheric deposition (Bobbink et al., 2010). Growth and competitive effect of *C. claviculata* seems to be promoted by this process (Van der Eerden et al., 1998; Lethmate et al., 2002). Additionally, soil disturbances and open patches in the herb layer of forests resulting from logging, tree fall gaps and, to a smaller extend, activity of animals may enhance nutrient availability through accelerated rates of mineralization (Brady and Weill, 1999).

C/N ratios of the humus layer found across the range on forest locations were around 30 in the Teutoburger Forest (Lethmate et al., 2002), 26 in E Brandenburg and 24 in NW Germany, 24 in central eastern part of the Netherlands and 25 in S Sweden (Voss et al., unpublished data). On shallow podzolic soils in France in Brittany with up to 20 cm thick organic layer there was a ratio of 21–25 (Clement et al., 1980).

Communities

In order to get an impression of the species composition in the different parts of the entire range of the species we assigned 920 vegetation relevés (for details see Voss et al., 2011) with *C. claviculata* from across the entire range to five climatic environmental zones (Metzger et al., 2005; for the zones see Table 2). These zones differed with respect to minimum and maximum temperature of the months January, April, July and October, precipitation during these months and oceanity (Metzger et al., 2005). For each zone the ten most frequent species of the herb/shrub layer and the five most frequent species of the tree layer were identified (Table 2). The most frequent (>25%) herb/shrub species across the entire range associated with *C. claviculata* were *Deschampsia flexuosa*, *Sorbus aucuparia*, *Quercus robur*, *Rubus fruticosus* agg. plus *corylifolius* agg., *Pteridium aquilinium*, *Frangula alnus*, *Holcus mollis*, *Rubus idaeus*, *Lonicera periclymenum*, *Stellaria holostea*, *Teucrium scorodonia*, *Dryopteris dilatata*, *Agrostis capillaris*, *Dryopteris carthusiana*, and *Vaccinium myrtillus*. The most frequently occurring (>10%) tree species were *Q. robur*, *Fagus sylvatica*, *Pinus sylvestris*, *Betula pubescens*, *B. pendula*, and *Ilex aquifolium*.

C. claviculata occurs in various forest communities in different parts of its range and is considered as character species of the acidophytic birch-oak forests in the order *Quercetalia roboris* Tx. 1931. In the map of the natural vegetation of Europe (Bohn et al., 2002/2003) all communities in which *C. claviculata* occurs belong to the macroclimatic zone "mesophytic deciduous broadleaved forests and mixed coniferous-broadleaved forests". This formation contains subgroups that differ with respect to species composition, climatic gradients and large scale habitat factors. These groups, in turn, are subdivided into different types with respect to nutrient regime, altitude, moisture regime and geographic location.

C. claviculata is diagnostic species or occurs as frequent species in the subgroups (1) "species poor acidophilous oak and mixed oak forest" (here the species occurs in communities at all altitudes), (2) "mixed oak ash forests" and (3) "species poor oligotrophic to mesotrophic beech and mixed beech forests".

1. Species poor acidophilous oak and mixed oak forest *lowland–colline (to submontane) types*:

- Atlantic-subatlantic birch-pedunculate oak forests (=F8 in Bohn et al., 2002/2003) in Belgium, Denmark, NW Germany, S Norway,

Table 2
Frequency (%) of the ten and five most frequent species (bold numbers) co-occurring with *Ceratocapnos claviculata* in the herb/shrub and tree layer (indicated by "T"), respectively, in five climatic environmental zones (Metzger et al., 2005) from across the entire range and the means of all groups. In deviation to Metzger et al. (2005), the zone Alpine South s.l. here comprises the original zones Alpine South, Mediterranean Mountains and Mediterranean North.

Zone	Continental	Atlantic North	Atlantic Central	Lusitanian	Alpine South s.l.	Mean
Number of relevés	110	259	444	69	38	920
Total species number	203	203	260	173	155	382
Betula pendula (T)	**10**	11	**11**	**22**	0	**11**
Betula pubescens (T)	**15**	**18**	**7**	4	**24**	**14**
Castanea sativa (T)	0	0	2	**16**	3	4
Fagus sylvatica (T)	7	**31**	**9**	**28**	**34**	**22**
Ilex aquifolium (T)	0	1	1	**22**	**29**	11
Picea abies (T)	**9**	**12**	2	1	0	5
Pinus sylvestris (T)	**54**	**22**	**24**	0	11	**22**
Quercus robur (T)	8	**57**	**35**	**46**	**13**	**32**
Robinia pseudoacacia (T)	**13**	0	0	1	0	3
Sorbus aucuparia (T)	2	6	3	7	**29**	9
Agrostis capillaris	**34**	16	23	**43**	18	27
Deschampsia flexuosa	**87**	**50**	**50**	**62**	**32**	**56**
Digitalis purpurea	5	5	19	**48**	24	20
Dryopteris carthusiana	**55**	**46**	**30**	3	3	27
Dryopteris dilatata	21	**56**	**39**	4	18	28
Dryopteris filix-mas	6	5	7	33	**37**	18
Erica arborea	0	0	0	7	**47**	11
Frangula alnus	**36**	**48**	**45**	23	8	**32**
Galeopsis tetrahit	19	31	24	**38**	3	23
Galium saxatile	20	16	12	**33**	16	20
Holcus mollis	8	22	**30**	**65**	**37**	**32**
Lonicera periclymenum	14	**43**	27	32	**34**	**30**
Molinia caerulea	17	35	**31**	9	0	18
Prunus serotina	**23**	25	**35**	0	0	17
Pteridium aquilinium	1	20	28	**45**	**76**	**34**
Quercus robur	**55**	**54**	**50**	17	3	**36**
Rubus fruticosus + *coryllifolius agg.*	**44**	**66**	**41**	1	21	**35**
Rubus idaeus	**59**	**47**	11	**35**	11	**33**
Sambucus racemosa	**25**	2	3	9	0	8
Sorbus aucuparia	**72**	**75**	**46**	28	3	**45**
Stellaria holostea	7	25	10	**38**	**66**	**29**
Teucrium scorodonia	0	3	25	**49**	**61**	28
Vaccinium myrtillus	17	**37**	17	17	**42**	26
Viola riviniana	0	2	3	17	**34**	11

S Sweden, The Netherlands and the Central UK. As diagnostic species there are e.g. *Q. robur*, *B. pendula*, *D. flexuosa*, *Melampyrum pratensis*, *Hieracium laevigatum*, *L. periclymenum*, *D. carthusiana*, *D. dilatata*, *V. myrtillus*.

- Atlantic-subatlantic hygrophilous birch pedunculate oak forests (F9) in N France, N Germany and The Netherlands with diagnostic species such as *Q. robur*, *L. periclymenum*, *F. alnus*, *Erica tetralix*, *Molinia caerulea*, *P. aquilinium*, *Aulacomnium palustre*, *Polytrichum commune*.

Colline-submontane types:

- Galician-north Lusitanian hyperoceanic pedunculate oak forests (F14) in NW Spain and NW Portugal with e.g. *Q. robur*, *Quercus pyrenaica*, *Ruscus aculeatus*, *Agrostis castellana*, *Daboecia cantabrica*, *Saxifraga spathularis*, *Viola riviniana*, *Blechnum spicant*.

Montane and altimontane types:

- Orocantabrian-northwest Iberian altimontane birch sessile oak forests and birch forests (F25) in N Portugal and NW Spain with e.g. *Quercus petraea*, *Betula pubescens* ssp. *celtiberica*, *Erica arborea*, *I. aquifolium*, *V. myrtillus*, *Doronicum carpetanum*, *Luzula sylvatica ssp. henriquesii*, *B. spicant*.

2. Mixed oak ash forests *colline-submontane types:*

- Cantabrian-Euscaldian mixed oak-ash forests (F33) in N Spain with e.g. *Fraxinus excelsior*, *Q. robur*, *Crataegus monogyna*, *C. avellana*, *Brachipodium sylvaticum*, *Arum italicum*, *Pulmonaria longifolia*, *S. holostea*).

3. Species poor oligotrophic to mesotrophic beech and mixed beech forests *lowland (-colline) types:*

- Norman-Belgian (sessile oak-) beech forests (F76) in N France, Belgium, The Netherlands (*F. sylvatica*, *Q. petraea*, *I. aquifolium*, *L. sylvatica*, *Digitalis purpurea*, *Rhytidiadelphus loreus*)

Colline-submontane types:

- Atlantic-subatlantic Luzula sylvatica-(sessile oak-) beech forests (F82) of the French Massif Central with (*F. sylvatica*, *I. aquifolium*, *Luzula forsteri*, *Euphorbia hyberna*, *Doronicum* spec. less frequent *Q. petraea*) (Bohn et al., 2002/2003)

As vegetation types in this system are relatively coarsely defined for Western and Central Europe which are the main regions of distribution of *C. claviculata*, we present these here in more detail:

In acidophytic birch-oak forests *C. claviculata* has its main occurrence in the associations *Deschampsio flexuosae-Quercetum roboris* Passarge 1966 (=F8 in Bohn et al., 2003) and *Betulo pendulae-Quercetum roboris* Tx. 1930 nomen inversum propos (=F8 und F9 in Bohn et al., 2003). In contrast to the latter, the *D. flexuosae-Q. roboris* Passarge 1966 is characterized by relatively dry, nutrient poor and little developed soils and lower species numbers. The *B. pendulae-Q. roboris* Tx. 1930 nomen inversum

Fig. 5. *Ceratocapnos claviculata* under different light conditions. (a) Habitus in a shaded forest site, (b) habitus in a sun-exposed forest clearing.

propos features boreal species such as *V. myrtillus* and partly *V. vitis*-idaea, *Maianthemum bifolium* and *Trientalis europaea* (Härdtle et al., 1997). In the UK, *C. claviculata* occurs in similar, atlantically distributed associations, namely the acidophytic communities of the *Quercus robur-Pteridium aquilinium-Rubus fruticosus* woodland on oligo- to mesotrophic brown earth of low base status or ranker, and the *Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa* woodland on oligotrophic podzols and stagnogley-podzols, often under slightly colder and moister climate (Rodwell, 1998; =F8 in Bohn et al., 2003). In France and Belgium, the species occurs in acidophytic, atlantic beech forests of the alliance *Ilici-Fagion* Braun-Blanquet 1966 (=F76 and F82 in Bohn et al., 2003). However, most of these stands are also rather *Betulo-Quercetum* communities (Härdtle et al., 1997; Heinken, pers. comm.).

In the course of changes of the forest management during the past century, in NW and Central Europe many original or near natural forests have been replaced by conifer plantations in the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. & al. 1939 (with spruce, douglas fir, larch, pine) or, but less frequently, plantations of *Robinia pseudoacacia*. Both forest types form substitute communities but exhibit partly a similar understorey composition (e.g. Rodwell, 1998; Decocq, 2000; Berg et al., 2001; but see Heinken, 1995). These conifer plantations occur on peat soils of disturbed bogs (Meyer and Voigtländer, 1996), on heathlands and inland dunes on sandy soils (Heinken, 1995). For the latter, pine forests of the type Dicrano-Pinion are characteristic and play a major role for the occurrence of *C. claviculata*. The species is characteristic for *D. flexuosa-P. sylvestris*-communities of relatively nitrogen and humus rich locations (Heinken, 1995). Within these it characterizes in Germany the atlantic(-boreal) *Galium saxatile*-vicariant (Heinken, 2008).

Although birch-oak forests are the most characteristic near-natural community types across the entire range, *C. claviculata* occurs often in higher abundance in ecotonal communities or under disturbed conditions (see chapter “Abundance”). Within the acidophytic forest clearing communities, stands with *C. claviculata* comprise the association *Corydalido claviculatae-Epilobietum angustifolii* Hülbusch & Tx. 1968 (Berg et al., 2001, 2004; Dengler et al., 2007); closely related communities are found in the UK or in France (Rodwell, 1998; Decocq, 2000). Another, permanent derivative of clearing and old coppice stands described for the UK is represented by the *Pteridium-Rubus* underscrub where *P.*

aquilinium can form the virtually completely closed canopy of the vegetation (Rodwell, 1998). Further ecotonal communities outside forests are along forest edges, hedges, roads, ditches and tracks. These stands may be assigned to different syntaxa within the *Origanetalia vulgaris* Th. Müller 1961, *Convolvulion sepium* Tx. 1947 and *Alliarion* Oberd. (1957) 1962 (Castroviejo, 1975; Jäger and Werner, 2005; BfN, 2010). Finally, the species occurs in dwarf-shrub heaths and sometimes even in pioneering, xerophilous communities on schist outcrops but under high air-humidity. In Brittany, these occurrences were attributed to the *Erico cinereae-Vaccinietum myrtilli* and the *Festuco-Sedetum anglici* (Clement and Touffet, 1977; Clement et al., 1980).

Response to abiotic factors

Due to its slender, hygromorphic habit the species is confined to either damp, but well aerated soils or sites of high relative humidity (see chapter "Habitat"). Especially seedlings respond very sensitive to drought. In a greenhouse experiment, germination was significantly higher in pots that were kept constantly moist than in those that were left to fall intermittently dry (47.2 ± 1.9% vs. 23.2 ± 2.7%, mean ± s.e.; t-test = 7.189, df = 18, $p < 0.001$) (Voss et al., unpublished data). These results are consistent with field observations: Germination success was significantly higher in populations in the native, oceanic range than in plots in the more suboceanic, invaded range which might be due to lower precipitation in the invaded range sites resulting in dry conditions during spring (Voss et al., unpublished data). However, adult individuals are able to tolerate drought despite their shallow roots as we observed vital, fruiting individuals (Fig. 5) on clearings without tree cover (average cover of *C. claviculata*: 8 vs. 4% in forests with a mean tree cover of 45%) and in common garden pot experiments (Voss et al., unpublished data).

Under field conditions, we found significant differences in specific leaf area (SLA, $m^2\,kg^{-1}$) between leaves of plants in shady, half-shady and sun-exposed sites in a population in S Sweden (Fig. 6). NE German localities were darker than the other sites which was reflected by a mean SLA of 63.99 $m^2\,kg^{-1}$. In contrast, in Swedish plants there was a mean SLA of 44.15 $m^2\,kg^{-1}$. This is equivalent to sunny and half-shaded sites and in fact, many of the Swedish populations were situated in forest clearings. Furthermore, individuals exposed to different light conditions were characterized by an overall different habit (Fig. 5). The development of thicker, more succulent summer and thinner winter leaves is also found in the closely related genus *Sarcocapnos* (Lidén, 1986).

In a controlled common garden experiment, we tested the effect of sun exposure on the response traits germination, SLA number of inflorescences, fruits and seeds, length, biomass, and seed mass through comparison of plants in sun-exposed (corresponding to situations in treeless open areas) and shaded pots (shading corresponding to situations in open forests). In order to take into account effects of geographic variability, seeds used for this experiment were obtained from plants of Spanish, Dutch, NW German, NE German and Swedish origin. In order to avoid maternal effects parental plants were grown in the greenhouse (for details see chapter "Germination"). The soil (Fruhstorfer Erde Typ P, Hawita-Gruppe, Vechta) that we used in the experiment contained 160 mg/l nitrogen.

Germination was significantly higher in shaded pots, which probably was due to a higher probability of desiccation in sun-exposed pots (Table 3). Under sun-exposed conditions leaf area per unit dry mass (SLA) was significantly smaller than for shaded plants. Furthermore, sun-exposed individuals flowered earlier than shaded plants. By mid-May, 61% of the sun exposed individuals were flowering but only 41% of the shaded individuals. Two weeks later all individuals were abloom.

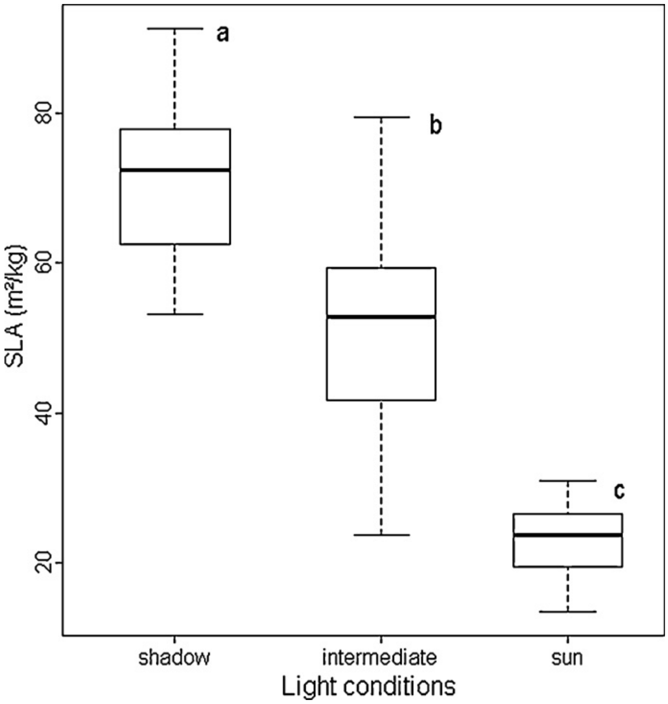

Fig. 6. Impact of light on specific leaf area (SLA, $m^2\,kg^{-1}$) of *Ceratocapnos claviculata*, measured in plants from shaded (whole day shaded), half-shaded (edge of the forest) and sun-exposed sites (clearing) in a population in S Sweden. Shown are the median, the lower and the upper quartile and minimum and maximum values. Letters a–c indicate significant groups (HSD test). ANOVA: $F_{2,73} = 50.216$; $p < 0.001$.

With respect to shoot length, shaded plants were significantly longer than sun exposed plants (Table 3). However, the number of seeds per capsule was slightly but significantly higher in plants of sun exposed pots and also the number of capsules was higher. In turn, seed mass was higher in shaded plants. However, no differences between the two treatments were found for number of inflorescences/individual and for above ground biomass.

In the same experiment, we studied the effect of the application of either 5 or 50 kg N per ha and year. There were no differences between fertilizer levels with respect to germination and shoot length. However, there was a positive response to fertilization of the number inflorescences per plant, biomass, and the number of seeds per capsule (Table 3).

(For information on soil requirements see chapter "Habitat", for response to low temperature see chapters "Phenology" and "Germination").

Abundance

In forests *C. claviculata* occurs with abundances ranging between 1 and 4% (references denoted by their IDs from the Global Index of Vegetation-Plot Databases (GIVD), Dengler et al. (2011), Heinken (2011a,b), ID EU-00-008; Rodwell (2011), ID EU-GB-001; May (2011), ID EU-DE-013 and Peppler-Lisbach (2011), ID EU-DE-010). However, in ecotonal communities, such as clearings, the species occurs with an average abundance of about 35% (Dengler et al., 2007). Especially on young clearfellings the entire area inclusive tree trunks may be covered by vital, intensely blooming, huge individuals, so that in places *C. claviculata* may be the most dominant plant species (Dengler et al., 2007; Voss et al., personal observation).

Table 3
Effects of the factors light (sun, corresponding to situations in treeless open areas, vs. shade, corresponding to situations in open forests) and nitrogen (application of 5 vs. 50 kg N ha^{-1} year^{-1}) on different fitness parameter of *Ceratocapnos claviculata*. Shown are mean, standard error (±s.e.), *F* statistic (*F*), *p*-value (*p*) and sample size (*n*).

	Sun		Shade				
Response variables	Mean	±s.e.	Mean	±s.e.	*F*	*p*	*n*
Germination (%)	28	23	12	11	103.7	<0.001	111
Shoot length (cm)	55.9	1.2	90.7	1.5	323.2	<0.001	95
SLA (m^2 kg^{-1})	35.3	1.2	75.3	2.3	333.8	<0.001	98
Capsules/inflorescence	9.7	0.3	8.8	0.2	11.91	<0.001	93
Seeds/capsule	2.19	0.06	2.00	0.04	6.122	0.015	99
1000 seeds (g)	1.088	0.022	1.004	0.018	19.12	<0.001	87

	50 kg N ha^{-1} year^{-1}		5 kg N ha^{-1} year^{-1}				
Response variables	Mean	±s.e.	Mean	±s.e.	*F*	*p*	*n*
Biomass (g)	3.7	0.2	2.7	0.2	12.82	<0.001	92
Inflorescences	73.4	3.8	55.3	3.4	10.77	0.001	98
Seeds/capsule	2.2	0.1	2.0	0.1	3.573	0.062	99

Life cycle and biology

Life cycle

C. claviculata is predominantly a summer- but also winter-annual semirosette therophyte (Buchenau, 1861; Voss et al., unpublished data). Due to this potential overwintering it is described as therophytic and partly as hemicryptophytic species (Moffat, 1923; Griffioen, 1961; Jäger and Werner, 2005). Seedlings of *C. claviculata* may emerge directly after dissemination in autumn (September) (Fig. 3). Under moist conditions in the greenhouse, we observed seeds that germinated only two weeks after dissemination. However, most of the seeds will not germinate before spring owing to a requirement for cold stratification to break seed dormancy (see also chapter "Germination"). The species propagates by seeds only and dies off after a large part of the seeds are mature and have been dispersed.

According to Ellenberg and Leuschner (2010), *C. claviculata* belongs to the small group of Central European liana-plants. The ability of climbing and winding is often found in plants with low Ellenberg continentality (=1) and high temperature values (=6) and in regions with long vegetation period, i.e. mild and short winters. The ability to climb enables the slender plant species to reach heights with better light conditions which may be advantageous in sites with well developed herb/grass layers.

The above ground dry biomass of plants sampled in four regions in Central Europe (The Netherlands, NW Germany, S Sweden and NE Germany) ranged from 0.04 to 32.5 g per individual, with a mean of 0.95 g (Table 2). Highest dry mass was found in populations from NW Germany, whereas plants from NE Germany were significantly smaller. These differences are most probably related to abiotic site conditions (lower soil moisture in NE Germany) rather than related to genotypic differences. Measurements of the number of inflorescences are in line with the former results: NE German individuals exhibited the lowest numbers (maximum 44 inflorescences) whereas the highest numbers were found in the more atlantic, western regions with 629 inflorescences in The Netherlands and 501 inflorescences in NW Germany. Furthermore, NE German individuals were shorter than those from the other regions. We measured a maximum of 83 cm in NE Germany and a maximum of 196 cm in S-Sweden.

The capsules may contain between one and four seeds (see also chapter "Morphology") but most capsules contain two seeds. However, in Spanish individuals we found a larger number of capsules with three seeds. Owing to constraints in resource allocation, seeds from Spain were lighter than those from all others regions.

Spatial distribution of plants within populations

In forest sites *C. claviculata* is found mostly in tens or hundreds of individuals. Here, the species occurs in small groups (Ellenberg et al., 1992; Voss et al., personal observation). In contrast, populations in fringe communities or in places where the species has newly established may consist of only a few individuals which may stand very close to each other. It is often difficult to identify what is a single individual because the species tends to become interwoven with its neighbors. On forest clearings or other disturbed sites, individuals may occur in high densities of thousands of individuals, occupying an area of several tens or hundreds of square meters (Voss et al., personal observation).

Phenology

Dierschke (1995) assigned *C. claviculata* to the symphenological *S. aucuparia-Galium odoratum*-group which predominately flowers at the end of full springtime.

Usually the species is abloom between (May) June and September which is about two to three months after germination (e.g. Corillion, 1983; Jäger and Werner, 2005; Voss et al., unpublished data). However, for Spain, a flowering period from March to October has been described (Castroviejo, 1998). Boulenger (1914) noticed blooming individuals in England already at the end of February and Weeda (pers. comm.) observed flowering plants in The Netherlands in January. This opportunistic flowering is probably facilitated by the mild winter climate in these atlantic localities (e.g. Du Buysson, 1914). *C. claviculata* may survive mild winters abloom and overwintering plants die already in June (Griffioen, 1961). This performance might be enabled by the sympodial shoot system (Fig. 2). In protected sites, e.g. under litter, shoots do not freeze and in spring the hibernating axillary buds cast out (Buttler, 1986). However, this behavior is not just confined to mild winters. Even after the very long and cold winter in 2008/2009, we observed huge not blooming individuals in E Brandenburg and S Sweden despite of temperatures of below −15 °C. This phenomenon was also observed by Lethmate et al. (2002) for N Northrhine Westfalia.

Reproduction

Like most other species in the tribe *Fumarieae*, *C. claviculata* is a synoecious, homogamic, self-compatible and autogamous species but it produces nectar and therefore is visited and pollinated by honey- and bumblebees (Lidén, 1986; Klotz et al., 2002; Voss et al., pers. observation).

The pollen is deposited on the stigma which is hidden between the apices of the inner petals. Flexible joints at the base of the inner petals allow them to be pressed down- or sidewards. By this mechanism the stigma will be exposed to the visitor. After the visit the petals resume their original position immediately (Lidén, 1986).

The gynoecium has 1–4 ovules (see chapter "Morphology") and across the range there are on average 2.2 (±0.1 s.e.) ovules per flower (Table 1). The androecium produces 488.9 (±13) pollen grains which results in a pollen/ovule ratio of 236.2(±9), which is less than 10% of the pollen/ovule ratios of related outcrossing species of Fumariaceae (Erbar and Langlotz, 2005) and thus suggests an autogamous breeding system (Michalski and Durka, 2009). As the species contains on average two seeds per capsule only about 9% of the ovules are aborted. An average individual may produce about 300 (21 inflorescences × 7 flowers/inflorescence × 2 seeds/capsule = 294) seeds (see Table 1 and chapter "Life cycle" for details on seed mass, number of capsules, seeds/capsule) but there may be also individuals with one single fruit or with almost 2000 seeds (N. Voss, personal observation).

C. claviculata seeds possess an inconspicuous aril (see chapter "Morphology"). Often, an aril is considered as an adaptation to myrmecochory. Horstmann (2005) found nests of *Formica polyetena* Foerst. in a location of *C. claviculata*. We never directly observed that ants transported seeds of *C. claviculata*. However, in the presence of ants between 10 and 65% of the seeds presented on the forest floor in Petri-dishes (mammals and birds were excluded through small meshed cages) were removed after 36 h (Voss et al., unpublished data). These field observations suggest that for short distance dispersal (within populations) entomochorous dispersal might be of importance for the species. However, for longer distances anthropochory or epizoochory, i.e. unintended dispersal through humans and animals, respectively, are probably the most important dispersal mechanisms which may explain its strong spread during the past decades (Voss et al., 2011). There are neither own observations nor information on endozoochorus dispersal of *C. claviculata*.

Germination

When the black, shiny seed of *C. claviculata* has imbibed water, the seed coat bursts open after a few days. One to two weeks later the hairy primary root appears. If sown on soil, the root is oriented straightly downwards into the soil. After further one or two weeks the two cotyledons are visible (Fig. 3).

In the family Papaveraceae (inclusive Fumariaceae) many species exhibit a combination of morphological and physiological dormancy (=morphophysiological dormancy; Grushvitzky, 1967). Probably this is also the case with *C. claviculata*: Buchenau (1861) described the embryo of *C. claviculata* as little differentiated at the time of dissemination (see chapter "Morphology"). This is in line with the observation that seeds germinated earliest two weeks after dissemination (see chapter "Life cycle"). Furthermore, at least for a large part of the seeds, cold stratification (cold pre-treatment) seems to be necessary in order to break physiological dormancy. In a climate chamber experiment with seeds from about 20 populations from each of the regions NW Germany and S Sweden, the impact of different stratification temperatures was tested. The seeds that we used in this and all following experiments described were harvested during a period of one month from parental plants which were cultivated in the greenhouse in order to minimize maternal effects. Seeds were slowly dried and stored for four weeks under dry conditions at room temperature before they were used in the first experiment. For the experiment 50 seeds per replication were put on moistened filter paper in a Petri dish. Germination was highest after stratification at 4 °C (35.0 ± 2.7%), here and below the standard error is given compared to stratification at 0° (23.7 ± 1.9) or 15 °C (12.4 ± 1.1; ANOVA: $F_{2,90} = 43.58$; $p < 0.001$; Chrzan et al., unpublished data). The results of this study are in line with the observation that the peak of germination occurs in spring after break of dormancy by low temperatures during winter. However, a small fraction of seeds does not need cold pre-treatment and thus, may already germinate in autumn, shortly after dissemination (see also chapter "Phenology").

Additionally, in a comparison of stratification period lengths, we found that germination increased at an alternating temperature of 10/20 °C with an increasing duration of the pre-treatment at 4 °C. If we exposed the moistened Petri dishes for two or four weeks to the cold treatment, only 14.3 (±3.5) and 17 (±4.5)% of the seeds germinated, respectively, whereas there were about 20.2 (±4.5) and 20.8 (±4.6)% seed germination after six and eight weeks, respectively (ANOVA: $F_{3,40} = 4.01$; $p = 0.014$). However, an extension of the stratification period to more than 8 weeks did not increase germination. Generally, the majority of seedlings emerged four to six weeks after the beginning of stratification (Voss et al., unpublished data).

Furthermore, we studied seed germination response to exposure to very low temperatures. We exposed seeds to a cold pre-treatment of −20 °C and transferred them afterwards to a temperature of 4 °C for germination. When the seeds were kept moist during stratification, 14.8 ± 1.1% of the seeds emerged afterwards. Without cold pre-treatment there was a germination of 43.6 ± 1.8% (LSD test; $p < 0.05$; $n = 20$). In contrast, when seeds were kept dry during stratification but moistened afterwards, germination was 50.9 ± 1.7% and 50.2 ± 1.2% with and without cold treatment, respectively (LSD test, not significant). Thus, very low temperatures by themselves do not damage seeds of *C. claviculata*, whereas imbibed seeds may be damaged through strong frost which, in turn, decreases germination success (Voss et al., unpublished data).

Generally, seeds of *C. claviculata* may germinate in darkness as well as in daylight, though there was a tendency for an increased germination in daylight (18.3 ± 2.0 vs. 20.1 ± 2.1%; ANOVA: $F_{1,64} = 3.752$, $p = 0.057$; Voss et al., unpublished data).

In contrast, highest germination success (71.2 ± 2.2% in Petri-dishes, at 4 °C) of *C. claviculata* was yielded with seeds which were not cultivated in the greenhouse but were collected in the field in NW Germany (Table 1).

Seeds of *C. claviculata* mostly are spread together with the indehiscent pericarp (Fig. 3). In a study with *C. heterocarpa*, germination success of seeds without pericarp was about five times higher than germination success of intact fruits. Adding pericarp to naked seeds did not decrease germination, indicating that an indehiscent pericarp might impede germination physically but not through inhibiting chemical compounds. Moreover water and gas access to the seed was guaranteed by cracks or when the apical beak had fallen off. Thus, in the field, an indehiscent pericarp provides a greater chance of survival by delaying germination (Ruiz de Clavijo, 1994). However, germination of seeds from *C. claviculata* was neither increased nor accelerated with pericarp compared to naked seeds (Buttler, 1986).

There was no information available on seed bank type (Thompson et al., 1997; Kleyer et al., 2008). However, *C. claviculata* was found in soil seed banks in old British coppice woods. In total, 5.4 seeds per m^2 of soil cores from a depth of 0–15 cm germinated within two years (Brown and Oosterhuis, 1981). We tested soil samples which were taken in six dense populations each in The Netherlands and NW Germany. At a soil depth of 1–15 cm in total 41.2 seeds per m^2 germinated. Of course, these seeds may also have been transferred into this depth recently by burying animals or may have been accidentally translocated through the soil corer. Though we could find the species in the soil sample, the few existing studies do not present strong evidence for a persistent seed bank.

Response to competition and management

C. claviculata belongs to a group of forest species, which were avoided by game and even benefited from browsing animals through the creation of a less dense vegetation layer (Förster, 1998). Moreover, game passes and resting places of wild boar not just create gaps in the vegetation layer but additionally disturb the soil surface and create optimum conditions for germination of *C. claviculata*. The strong increase of populations of wild boar during the past decades might have even reinforced this effect (Ellenberg and Leuschner, 2010). Locations with intensive forestry management and clearfellings exhibit a similar disturbance but usually over much larger areas, and germination and establishment of ruderals and light-demanding species such as *C. claviculata* are promoted in these communities (Schultze-Motel, 1986; Berg et al., 2004; Dengler et al., 2007).

In contrast, in locations with dense vegetation layer the species exhibits a very slender growth and the abundance of the species may be low. However, the tendrils enable partly an overgrowing of the surrounding vegetation and there, light conditions are better for growth of *C. claviculata* (Lethmate et al., 2002).

Herbivores and pathogens

The weevils (Curculionidae) *Procas granulicollis* Walton, also known as Climbing *Corydalis* weevil, and *Sirocalodes mixtus* Mulsant & Rey are feeding on *C. claviculata*. The former is found only in Great Britain and Spain (Thompson, 2006). In Britain the nocturnal *P. granulicollis* often occurs in woodland clearings. According to Fowles (1992), *C. claviculata* is the sole recorded adult food plant of the weevil. It is leaving characteristic half-moon-shaped holes on the edge of the leaves. According to the EICA hypothesis (Blossey and Nötzold, 1995) release of enemies such as predators or herbivores in the newly invaded range may enhance the expansion process of species. However, although we observed feeding tracks of this form in several populations in the native range in The Netherlands and less often in all other study regions, we never observed neither of the weevils on the species (Voss et al., unpublished). Such damages can also be caused by slugs and caterpillars. A large number of caterpillars of the generalist species *Noctua pronuba* L. (Large Yellow Underwing) were found in a greenhouse cultivation of *C. claviculata* (Voss et al., personal observation).

The thermophile, herbicole weevil *S. mixtus* occurs from W Europe (but also in N Germany, Austria and Turkey) to N Africa predominantly on ruderal sites (Hoffmann, 1954; Lohse, 1983; Koch, 1992). It was first reported in the Netherlands in 1993 and appeared to be common on *C. claviculata* and *Fumaria officinalis* (Heijermann and van den Berg, 1995).

Furthermore, in cultivations and in populations in the Netherlands, infestation of the species by aphids could be observed (Voss et al., personal observation).

Mycorrhiza

Very often species on acidic soils show mycorrhizal infection. So far, there is no information concerning mycorrhizal infection for *C. claviculata*.

Physiological data

Most of the seeds are dormant and will only germinate after cold stratification (see chapter “Germination”). Otherwise there is no information available on the physiology of the species.

Biochemical data

Papaveraceae (inclusive Fumariaceae) are one of the few large plant families in which the formation and storage of phenylisoquinoline alkaloids could be detected in all analyzed genera (Hegnauer, 1969). In many species (such as *Corydalis*, *Dicentra*, *Fumaria*, *Ceratocapnos*) alkaloids are bound to fumaric acid and are stored in the vacuole of alkaloid idioblasts (Hegnauer, 1969).

The alkaloid chemistry strongly supports the subtribal classification of Fumariae. The compounds protopine, sanguinarine and coptisine are very common and they have the status of subfamily characteristics in Fumarioideae; the compound cularine is only found in this subfamily (Lidén, 1993; Nuhn, 2006). Apart from alkaloids, in this subfamily the flavonoid and aminoacid delta-acetylornithin could be detected which may serve as a transport form of nitrogen. Furthermore small amounts of arginine and glutamine are present (Hegnauer, 1969).

Up to now, more than 50 alkaloids could be detected in *C. claviculata* (Table 4). It has the following compounds in common with the closely related genus *Sarcocapnos*: celtin, celtisine, breoganine; sarcocapnidine, oxosarcocapnidine, calviculine, sarcocapnine, oxosarcocapnine, crassifoline, 4-Hydroxycularine, limousamine, ribasin and ribasidine (Hegnauer, 1969; Boente et al., 1983a). In *C. claviculata* the alcaloid fraction consists mainly of cularine, cularidine and cularicine whose occurrence is limited to Fumariaceae (Blaschke and Scriba, 1985). Cularine is described as a relaxatant against contractions in the human bronchus thus having antispasmogenic activities (Candenas et al., 1990). Furthermore it may produce anesthesia of the cornea, a drop in blood pressure, an increase of heart tone and heart contractility, it has an effect on smooth muscles by stimulating the uterus and depressing the intestinal motility (Reynolds, 1940; Blaschke and Scriba, 1985). Finally cularines possess a similar arrangement of the nitrogen–oxygen–oxygen bonds as found in antineoplastic agents and thus they might have a similar impact (Castedo and Suau, 1986). Cularidine (and also reticuline) work inhibitory on smooth muscles and due to this cause vasorelaxation (D’Ocon et al., 1991; Paulo et al., 1992).

Some of the alkaloids in *C. claviculata* like crassifoline or cularine serve only or partly as precursors for other alkaloidic compounds like cancentrine or noyaine (Boente et al., 1983b; Blaschke and Scriba, 1985).

In general, isoquinoline compounds account for resistance against phytopathogenic organisms and many of them are pharmacologically active for which reason they were already used in ancient times as antiseptics, analgetics, antispasmodics, sedatives and laxatives (Blaschke and Scriba, 1985; Hao and Quicheng, 1986; Kuo et al., 2004). Some of the protoberberines (berberine, coptisine, protopine, scoulerine and stylopine), dihydrosanguinarine and isoboldine have cytotoxic activities and thus may have antiulcer, antibacterial or antifungal activity. Furthermore, some of them were detected to contain chemicals which may work as defense against arthropods (Leitao da-Cunha et al., 2005; Veldman et al., 2007; Vrba et al., 2009).

Interestingly, the compounds culacorine, norcularicine and oxocularine could only be isolated in individuals of *C. claviculata* from the surroundings of Limoges by a French group (Allais and Guinaudeau, 1983) but were not found in collected plants from

Table 4
Alkaloidic groups and compounds found in *Ceratocapnos claviculata* (Boente et al., 1983a,b; Boente et al., 1984a,b; Blaschke and Scriba, 1985; Boente et al., 1986a,b; Castedo and Suau, 1986; Allais and Guinaudeau, 1990).

Alkaloidic group	Compound
Aminoethylstilbene	Crassifoline methine, leonticine (=petaline methine)
Aporphine	(+)-Isoboldine, thaliporphine
Benzophenanthridine	Dihydrosanguinarine
Benzyltetrahydroisoquinoline	(+)-Crassifoline, (+)-juziphine, (+)-reticuline
Cancentrine	(+)-Claviculine, oxosarcocapnidine, (+)-sarcocapnidine, sarcocapnine, oxosarcocapnine
Cularine	Breoganine, celtine, celtisine, (+)-corycularicine, (+)-culacorine, (+)-cularicine, o-methylcularicine, oxocularicine, (+)-norcularicine, (+)-cularidine, (+)-norcularidine, cularimine, (+)-cularine, oxocularine, (+)-enneaphylline, sauvagnine, dihydrosauvagnine, secocularidine
Dibenzazonine	Crassifolazonine
Dibenzofuranazepine	Clavizepine,
4-Hydroxycularinalkaloids	Hydroxycularine, (+)-limousamine, hydroxysarcocapnine
Indanobenzazepine	(+)-Ribasine [=(+)-limogine], (+)-norribasine, ribasidine
Morphinanedienone	(−)-Pallidine
N-Benzyltetrahydroisoquinoline	Viguine
Proaporphine	(−)-Glaziovine
Protoberberine	Berberine, (−)-cheilanthifoline, coptisine, 8-oxycoptisine, (−)/(+)-stylopine, (−)-scoulerine, (+)-protopine
Secocularine	Norsecocularine, noyaine

the surroundings of Bremen by Blaschke and Scriba (1985). On the other hand the compounds claviculine, crassifoline, cularimine and sarcocapnidine were described in German but not in French specimens. These differences might be due to measuring inaccuracies but according to Blaschke and Scriba (1985) also chemical races might be the cause of such differences.

Genetic data

Like in *C. heterocarpa*, the chromosome number of *C. claviculata* is $2n = 32$ (Reese, 1951; Ryberg, 1960; Gadella and Kliphuis, 1966; Queiros, 1981; Lidén, 1986; Elena Rosselló et al., 1987). Assuming a basic chromosome number of $x = 8$, the species is tetraploid (Klotz et al., 2002). However, in a single literature source, in addition also $2n = 64$ was mentioned (Queiros, 1981). In *Fumarieae* chromosomes have a length of less than 1 μm. In *Corydaleae* each chromosome measures about 2 μm which is in line with inbreeding annuals usually having smaller chromosomes than outbreeding perennials (Lidén, 1986).

Hybrids

As there are no close relatives across the current range there is no information on hybridization. However, in the tribe Fumarieae almost all species have strong intersterility barriers (Lidén, 1986).

Status of the species

Across the entire range, the species is neither economically used nor under protection. In fact, during the last four decades a spread within its native range such as in the UK (Hill et al., 2004), in N Belgium (Vannerom et al., 1994) and NW Germany (Pott and Hüppe, 1991; Pott, 1990; Jäger and Werner, 2005) has been noted. Furthermore, the species showed also a strong expansion eastwards- and northwards towards suboceanic and north-temperate regions and established a number of populations in N France (Decocq, 2000), in NE North Rhine Westphalia (Pollmann and Lethmate, 2006), Mecklenburg-Western Pomerania (Meyer and Voigtländer, 1996), NE Lower Saxony (Dengler et al., 2007), NW Saxony-Anhalt (Passarge and Hofmann, 1968; Rattey, 1984) and Brandenburg (Benkert et al., 1995) in Germany, as well as in Skåne and Blekinge in S Sweden (Hylander, 1971; Oredsson, 2005). Occasional populations are also found in NW Bavaria, Rhineland Palatinate, Hesse, E Thuringia, Saxony (Jäger and Werner, 2005) and Austria (Kleesadl, 2009).

A common character of all these sites is that they originally have been acidic beech or birch-oak forests but now changed to rather non-natural (e.g. stands of *Pseudotsuga*, *Pinus*, *Larix*, *Robinia*) or non-constant forest communities, clearings or disturbed sites (Pott, 1995; Benkert et al., 1995; Pollmann and Lethmate, 2006; Ellenberg and Leuschner, 2010). Additionally, the species occurred in most of the sites spontaneously, often with distances of 10–100 s km from the next population and in higher abundance than in native range sites (Rattey, 1984; Voss et al., 2011, Fig. 1).

Possible causes for the successful establishment might be increased nitrogen depositions combined with soil acidification and, especially towards the East, milder winters of the last decades (shift of the 0 °C isoline towards Northeast) due to global change (Bobbink et al., 2010; Pott, 1990; Decocq, 2000; Lethmate et al., 2002; Parmesan and Yohe, 2003). However, this alone does not explain the fast expansion over long distances and occurrence of isolated populations. Thus, direct anthropogenic activities such as transport of wood and forest saplings from tree nurseries, afforestation and clearcutting in the course of intensive forest management, and disturbance of the vegetation layer and soil surface might have the largest influence on successful dispersal and establishment of the therophytic species (Buttler, 1986; Decocq, 2000; Oredsson, 2005; Voss et al., 2011; see also chapter "Reproduction"). E.g. occurrences in Sweden might be related to seeds or fruits which were attached to timber bark and which was transported as pulpwood and sawtimber to Swedish sawmills and paper plants after severe storms in NW Germany and The Netherlands in the 70 s (Buckley et al., 2003; Oredsson, 2005). Once introduced, secondary factors such as atmospheric nitrogen deposition or milder winters may facilitate successful establishement of the species.

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