Two shades of grey: effect of temperature on seed germination of the escaping ornamental species *Lychnis coronaria* and *Stachys byzantina*

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**Abstract** This paper describes germination and cytological variability in two popular ornamental and potentially invasive species, lamb’s ear *Stachys byzantina* and rose campion *Lychnis coronaria*. Both xerophytic species have the potential to invade natural habitats across Europe and create viable naturalised populations, with subsequent impacts on native vegetation. To assess the species’ invasiveness, seeds were collected from naturalised populations and germination was recorded under different temperature regimes. Flow cytometry, used to record cytological variability, indicated that all populations of both species were cytologically homogeneous. Germination success, an important means of distribution factor in both species, was significantly influenced by temperature, with final germination of *L. coronaria* being extremely high at temperatures > 15/10 °C (98.5%) and extremely low at temperatures < 10/5 °C (2.9%). The final germination in *S. byzantina* is the highest at 22/15 °C (55.6% germinated seeds), reduced to 40.3% at 15/10 °C and to 0.3% at temperatures lower than 10/5 °C. No significant differences in final germination were observed between escaping and non-escaping populations, although there were some differences between particular populations. Our results indicate germination temperature limits of two species whose non-native areas include Central Europe. The observed germination allows for successful generative reproduction of both species over their non-native ranges, suggesting that these species are likely to become invasive species of European grasslands soon.

**Keywords** Alien species · Generative reproduction · Genome size · Lamb’s ear · Ornamental plants · Rose campion

**Introduction**

Horticulture has been an integral part of human society for centuries (Relf and Dorn 1995; Zhou 1995; Kendle and Stoneham 2014). Recently, however, the increasing influence of horticulture has made it one of the major sources of alien plant species (Dehnen-Schmutz and Touza 2008; Klonner et al. 2017; van Kleunen et al. 2018; Vojík et al. 2020). These not
only contribute significantly to regional floral communities (Köppler et al. 2014; Lososová et al. 2015; Pergl et al. 2016), they also potentially threaten biodiversity and natural ecosystems, leading to the homogenisation of the Earth’s biota (Vilà et al. 2011; Price et al. 2018; Morri et al. 2019; Pyšek et al. 2020). The control and eradication of such ‘invasive species’ are demanding and often unfeasible (Ewel and Putz 2004; Downey et al. 2010) and, as such, it is crucial to prevent the spread of potentially invasive species before they get a hold (van Kleunen et al. 2007). Whether a species becomes invasive depends not only on the species’ ecology but also on the physical characteristics of the invaded habitat and the prevalent environmental conditions (Pyšek et al. 2012a). One of the most important ecological traits to assess when investigating the potential for invasion in early spreading species are their reproduction traits, i.e. whether they can be a ‘master of all traits’ or if they have specific characteristics leading to their success (Pyšek 2007; Pyšek et al. 2009). Species reproducing by seed tend to be associated with habitat conditions such as light availability and temperature regime, with low temperatures limiting germination and day length influencing seedling establishment (Pepe et al. 2020). However, species that are capable of germinating at lower temperatures, with earlier timing of germination and rapid seedling growth, will have a competitive advantage over other species (Baskin and Baskin 1998). Furthermore, species with wider distributional ranges can have competitive advantages due to adaptation to different conditions of their local populations across the range. The germination of these species is usually tested in the different temperature regimes to define their germination niche breadth (Brändle et al. 2003). This parameter, combined with others (ecological niche breadth, geographic range etc.), can result in ecotypic differentiation detectable by germination tests (Donohue et al. 2010). The ecotypic differentiation represents an opportunity for increasing species’ fitness (e.g. Geber and Eckhart 2005). Recent studies focused on reproduction traits have often concentrated on variability within the genetic structure of plant populations (e.g. Saad et al. 2011). High genetic and cytological diversity of introduced populations increases species survival capacity (Puillandre et al. 2008; Estoup et al. 2016). If the introduced population is small, however, it may have a low level of variability, creating a bottleneck effect that could limit its invasion success (Puillandre et al. 2008). Nevertheless, some introduced species have become invasive with a low level of genetic/cytological diversity due to a so-called ‘genetic paradox of invasion’ (Hassan et al. 2003; Dlugosch and Parker 2008b; Estoup et al. 2016), whereby genome size and polyploidy in newly spreading alien species may be the first indication of increasing variability or ongoing evolutionary processes, which could then support invasion (Meyerson et al. 2020; Wan et al. 2020). Due to polyploidization, faster germination can occur (e.g. Bretagnolle et al. 1995), which can support the spread and thus increase the invasive potential of some populations. The effect of polyploidization on the germination of invasive and potentially invasive plants has already been demonstrated (e.g. Castro et al. 2007; Pegtel 1999).

Other characteristics aside from reproduction traits have also been identified as significantly affecting invasion/naturalisation probability in ornamental taxa (Pyšek et al. 2019). For example, the horticultural success of certain species is mainly related to their charisma (e.g. colour, shape and size of bloom, or time of flowering), which affects not only global public perception but also introduction by humans and resistance to management following their escape (McNeely 2001; Shackleton et al. 2019; Jarić et al. 2020). The invasion potential of ornamental species following introduction will then be linked to their ability to grow under low maintenance (e.g. abandoned sites) and their adaptability to local conditions (e.g. temperature, humidity), such characteristics also giving the species a greater ability to escape from horticulture (Williams et al. 2010; Flory et al. 2011; Vojík et al. 2020; Kutluvašr et al. 2020). There have also been several recent cases of ornamentals spontaneously spreading due to global warming, highlighting the potential of climate change to facilitate invasions (Dullinger et al. 2017; Haeuser et al. 2018).

In this study, we describe germination and cytological variability in two popular ornamental and potentially invasive species, lamb’s ear Stachys byzantina and rose campion Lychnis coronaria, whose status are casual and naturalised, respectively, in the Czech Republic (Pyšek et al. 2012b) and have spread into human-made habitats (e.g. mown lawns or grasslands). Both species are popular ornamentals worldwide due to their grey-felted leaves and easy maintenance, and have been planted in a wide range of habitats, including public parks and private...
gardens as well as courtyards (Dimke et al. 2008; Wade and Mengak 2010; Cullen et al. 2011; Glawe and Koike 2018). Records of both species escaping from cultivation have increased in recent years, with such escapes going on to form viable populations in both artificial and semi-natural habitats (Barošová and Baroš 2009; Kutlvašr et al. 2019; Vojík et al. 2020), including narrow and broad-leaved dry grasslands and acidophilous dry grasslands. Consequently, these species can be considered as newly emerging alien species that could easily become invasive. Moreover, in the case of S. byzantina, hybridisation may be possible with an endangered native species, Stachys germanica—Endangered category (C2b) on the IUCN Red List of endangered species (see Grulich 2017), which is known from the literature (Dunn 1997) and which has recently been recorded in the Czech Republic (Danihelka in prep.). Hybridisation, alongside effective generative reproduction, could significantly accelerate the invasive success of S. byzantina by producing high performance genotypes that could rapidly colonise even unfavourable sites (see Buňk and Thielsch 2015).

Though both species originate in the Middle East, they differ in their native range (POWO 2019). It has been shown repeatedly that the probability of naturalisation success is affected by the size of a species’ geographical range and its habitat range niche (e.g. Rejmánek 1996; Pyšek et al. 2009). With a native distribution centred on the Mediterranean and Central Asia, L. coronaria has a sizeable native range with a broad ecological amplitude (Hejny 1997; CABI 2019; Chytrý et al. 2021) unlike S. byzantina, which is an endemic species to Iran (Asnaashari et al. 2010). While the basic descriptive characteristics regarding biology and ecology are known for both species (see Hejny 1997; Chytrý et al. 2021), details on population variability and their ability to spread remain largely unknown.

To identify reasons for the recent spread of both species, we undertook a series of tests to assess cytological variability and in vitro seed germination potential. In doing so, we asked a series of questions: (1) What is the genome size variability among populations of two individual species S. byzantina and L. coronaria? (2) Is the germination of either species affected by temperature? (3) Are there any differences between escaping and non-escaping populations in seed germination? (4) Where is the temperature limit of generative reproduction of the species?

Material and methods

Study species

Stachys byzantina C. Koch (Lamiaceae) is a perennial, long-felted, 20–80 cm tall herb. It is diploid (2n=30; Hejny 1997; Lindqvist and Albert 2017; Wild et al. 2019). Originally an endemic Iranian mountain species (Asnaashari et al. 2010), it has widened its native area to include north Turkey and the Crimean Peninsula (POWO 2019). It has been introduced to Central and Western Europe, North America, Canada and New Zealand (POWO 2019). Germination characteristics of S. byzantina are not available; however, generative and clonal reproduction has been observed in the field (Vojík et al. 2020). Based on numerous field observations, it is obvious that the species is a polycarpic perennial, which is stated to be probably myrmecochorous (Chytrý et al. 2021) with Allium dispersal type (mostly autochory; see Šádlo et al. 2018). Information about self-fertilization is unknown but could be expected because of self-fertilization ability in the related species Stachys germanica (Minachilis et al. 2021).

Lychnis coronaria (L.) Desr. (Caryophyllaceae) is a short-lived, white felted, monocarpic perennial plant, generally grown as a biennial or annual, 30–60 (–100) cm tall (Jiang et al. 2016; Moravcová et al. 2010). It is diploid (2n=24; Hejny 1997; Jeelani et al. 2011; Zonneveld 2019). It originates from the Mediterranean, Middle East and the whole of Central Asia. The northern boundary of the native range reaches southern Slovakia. It is non-native in Central and Western Europe and North and South America (Brazil, Chile; Hejny 1997; POWO 2019). The final germination percentage of L. coronaria is 100% under tested laboratory conditions (12 h in light/12 h in the dark; 25/10 °C, 20/5 °C and 15/5 °C), with seedling establishment reaching almost 60% (Moravcová et al. 2010). Life-history strategy of the species was classified as CSR (Klotz et al. 2002) with an Allium dispersal type (mostly autochory; Šádlo et al. 2018; Klotz et al. 2002), non- myrmecochorous (Chytrý et al. 2021). Information about self-fertilization is unknown but could be expected due to
self-fertilization in related species *Lychnis flos-cuculi* (Dulya and Mikryukov 2016).

Population genome size variability

Within sampling design for assessment of genome size, we used 7 populations for *L. coronaria* and 10 populations for *S. byzantina* (see Online Resource table); all these populations were also selected for germination experiments (at random)—for genome size analysis, fresh leaves were used from particular maternal plants in populations from the Czech Republic. The two populations from the native range (LC5—Istanbul, TR and SB10—Tehran, IR) were germinated first and then seedlings were used for the genome size analysis.

To assess genome size homogeneity, the DNA weight per nucleus (genome size; expressed in picograms [pg]) was determined for each study population (see Online Resource table) using flow cytometry, based on a two-step procedure using Otto I and II buffers (Otto 1990). As its genome size (2C DNA = 3.38 pg) is close to that of the species studied, the common daisy *Bellis perennis* was used as an internal reference standard (Schönswetter et al. 2007). In each case, 1 cm² of fresh leaf tissue from the study species and from *B. perennis* were macerated together with a sharp blade and placed in a Petri dish containing 0.1 ml of ice-cold Otto I buffer (0.1 M citric acid monohydrate, 0.5% v/v Tween 20) for approx. 90 s, after which the suspension was filtered through a 42 µm nylon mesh. Nuclei within the filtered suspension were then stained with 1 ml of Otto II buffer (0.4 M Na₂HPO₄ 0.12H₂O) supplemented with 1 ml of DAPI stock solution (DAPI 10 mg dissolved in 100 ml H₂O) + 50 µl β-mercaptoethanol (2 µL/mL). Each sample was then incubated at room temperature for 10 min and analysed using a Sysmex-Partec CyFlow SL equipped with a green solid-state laser flow cytometer (532 nm, 100 mW output power; Sysmex Partec GmbH, Görlitz, Germany).

Seed collection and germination experiments

Two germination experiments were undertaken, the first assessing the effect of temperature regime on seed germination, and the second assessing differences in final germination between escaping and non-escaping populations. The populations were selected randomly in the Czech Republic at sufficient distances from each other (more than 500 m) to not collect the seeds from one population repeatedly (detailed locations are in Online Resource table). Seeds were collected from the 10 most viable and fully matured plants per population. The required number of healthy-looking and fully sized seeds was selected for germination experiments (i.e. *L. coronaria*: 360, *S. byzantina*: 270 seeds). The seeds from the Czech Republic were collected at the end of the growing period 2017 (*L. coronaria*) and 2018 (*S. byzantina*). Moreover, the seeds from three distant populations were also collected in defined years— one from the native range of *L. coronaria* in 2017 (LC7; Istanbul, Turkey), one from the non-native range of *S. byzantina* in 2018 (SB9; Dublin, Ireland), and one from the native range of *S. byzantina* in 2018 as well (SB10; Tehran, Iran). Because the longevity of the seeds can be significantly different (e.g. between families or localities; Walters et al. 2005), we used fresh seeds for the experiments, which were first dried at room temperature (ca. 20 °C) for a week. Furthermore they were dark-stratified at 5 °C for six weeks to simulate the winter period in Central Europe (e.g. Mandák et al. 2006; Kołodziejek 2019), then surface-disinfected in 70% (v/v) ethanol for 1 min and immersed in 50% (v/v) bleach solution for 1 min as well (<5% sodium hypochlorite; Šlesak et al. 2017). The seeds were then incubated in Petri dishes on three-layers of filter paper dampened with distilled water. Seeds were kept under a simulated daily light regime consisting of 14 h light and 10 h dark with four different temperature regimes, 22/15 °C, 15/10 °C, 10/5 °C and 5/3 °C. The 5/3 °C regime was used only for *L. coronaria* as our previous screening experiment had shown that *S. byzantina* seeds stop germinating at 10/5 °C. Each population sample consisted of 30 seeds in three replicates for each group (escaping vs non-escaping) or treatment (temperature regimes). All germinated seeds were counted and recorded at two-day intervals for 30 days. The experiment was performed in complete randomized blocks and the individual temperature regimes were applied in a factorial design.

To evaluate the effects of temperature regime on seed germination, we collected seeds from four *L. coronaria* populations and four *S. byzantina* populations. The populations were selected on semi-shaded human-made habitats (e.g. backyards, gardens and
parks) in environmental conditions typical for central Europe (average precipitation 450–712 mm, 7–9 °C; see Online Resource table) for reducing the differences among populations. Three germination traits were measured: (1) final germination, calculated as the total number of germinated seeds at the end of the germination period, (2) germination rate, calculated as the number of germinated seeds in each time interval, and (3) germination delay (hereinafter GD), calculated as the number of days until the first germination recorded (Cerabolini et al. 2004; Pepe et al. 2020).

To compare differences in final germination between escaping and non-escaping populations (only this germination trait was measured here), seeds were collected from maternal plants, i.e. even in the case of escaping populations maternal plants growing in gardens were sampled (the cultivated source populations). The sampling design was the same as for the first trial and the populations were selected independently on environmental conditions. Both groups (escaping vs. non-escaping) were sampled in the same year for particular species (L. coronaria—2017, S. byzantina—2018). Eight S. byzantina populations were sampled, four escaping and four non-escaping, and six L. coronaria populations, four escaping and two non-escaping (see Online Resource table). Escaping populations were characterised by intensive spontaneous spreading into surrounding semi-natural grasslands, while non-escaping populations showed no sign of spreading, despite suitable habitats for spontaneous spreading being available. Differences in final germination between escaping and non-escaping populations were tested using seeds grown in the 22/15 °C regime, as this was shown to be optimal for both species during the first experiment of this study, where it was tested in different temperature regimes (see above).

Data analysis

Differences in final germination between temperature regimes were tested by comparing observed ‘final germination’ counts using generalized linear mixed-effect models (GLMM) for the negative binomial family. Temperature regimes were included as a fixed factor. The same models were used to assess differences in final germination between escaping and non-escaping populations of each species, using the number of germinated seeds as the response variable and escaping/non-escaping as the predictor (fixed effect). GLMMs were also used for GD analyses using the number of days until first germination recorded as a response variable and different temperature regimes as a predictor (fixed effect). Particular populations were included as a random effect and hierarchically nested within the fixed effect in all GLMMs. Full models were simplified using posterior comparisons and the most plausible models were selected based on the Akaike information criterion (Akaike 1978; Crawley 2012), using backward selection.

Differences in germination rate were tested using MANOVA (multivariate ANOVA) due to the violation of the sphericity assumption (assumption for the use of repeated measures ANOVA), where the number of germinated seeds at a particular time was used as the response variable, temperature regimes were multivariate used as predictors (Mardia et al. 1979; Lepš and Šmilauer 2016).

All analyses were performed using R software (R Development Core Team 2019) and Statistica 13 (TIBCO 2017), with differences considered significant at $P \leq 0.05$.

Results

Population genome size variability

Flow cytometric analysis confirmed genome size homogeneity in all populations of both species in their non-native range (Fig. 1), with S. byzantina populations ranging from 1.55 to 1.63 pg (2C-values), and L. coronaria populations ranging from 6.40 to 6.58 pg (2C-values) (see Online Resource table).

Seed germination

*Lychnis coronaria*

Temperature had a highly significant impact on final germination, with posteriori comparisons distinguishing two levels of significance, i.e. $< 10/5$ °C ($\bar{x} \pm SE; 0.88 \pm 1.83$; SE: Standard Error of Mean) and $> 15/10$ °C (29.54 ± 0.91) (average per Petri dish; Fig. 2a). While germination at temperatures $< 10/5$ °C was low, with final germination at 2.9% (21 of 720 seeds germinating), final
germination at temperatures > 15/10 °C was exceed-
ingly high at 98.5% (709 of 720 seeds germinating).

GD was significantly affected by temperature. Seeds germinated later at lower temperatures,
with a GD of three days at 22/15 °C, three days at
15/10 °C, nineteen days at 10/5 °C, and no germina-
tion at 5/3 °C. The seed germination rate over the
first twelve days differed significantly, primarily due
to population LC2 having a lower germination rate
at 22/15 °C, though this difference later vanished
(Fig. 3).

All detailed results are merged in Table 1.

Stachys byzantina

As with L. coronaria, temperature had a highly sig-
nificant impact on final germination. Likewise, ger-
mination was low at temperatures < 10/5 °C, with
a final germination of 0.3% (1 of 360 seeds germi-
inating), but increased with increasing temperature,
with final germination at 15/10 °C reaching 40.3%
(145 of 360 seeds germinating) and the highest final
germination being recorded at 22/15 °C at 55.6%
(200 of 360 seeds germinating) (Fig. 2b). No seeds
germinated at 10/5 °C (apart from one seed from the SB3 population).

GD was significantly affected by temperature. Seeds germinated later at lower temperatures, with a GD of two days at 22/15 °C, seven days at 15/10 °C and just one seed germinating at 10/5 °C.

There were significant differences in seed germination between temperatures over time, with the strongest effect observed at higher temperatures, i.e. 12.08 ± 8.21 at 15/10 °C and 16.70 ± 5.93 at 22/15 °C (average per Petri dish). Populations SB1 and SB4 both displayed a higher germination rate than the other populations, with almost all seeds germinating during the first ten days of the experiment (Fig. 5).

**Table 1** Results of all germination trials of *Lychnis coronaria*

| Tested parameter          | df  | Test statistics | P value |
|---------------------------|-----|-----------------|---------|
| Temperature regime        | 1, 43| $z = 15.894$    | < 0.001 |
| Germination rate          | 42, 93| $F = 4.335$    | < 0.001 |
| Germination delay         | 2, 43| $z = -12.784$   | < 0.001 |
| Escaping                  | 1, 5 | $z = 0.157$     | > 0.05  |

$df$ degrees of freedom
Significant effects ($P < 0.05$) are indicated in bold

**Table 2** Results of all germination trials of *Stachys byzantina*

| Tested parameter          | df  | Test statistics | P value |
|---------------------------|-----|-----------------|---------|
| Temperature regime        | 2, 30| $z = 4.959$     | < 0.001 |
| Germination rate          | 28, 40| $F = 4.367$    | < 0.001 |
| Germination delay         | 2, 30| $z = -6.901$    | < 0.001 |
| Escaping                  | 1, 7 | $z = -0.073$    | > 0.05  |

$df$ degrees of freedom
Significant effects ($P < 0.05$) are indicated in bold

Difference in final germination between escaping and non-escaping populations

There was no significant difference in final germination between escaping and non-escaping populations of particular species.

All detailed results are merged in Table 2.
Discussion

Detailed studies of generative reproduction and population ecology, including studies of genetic and cytological variation, have proved to be promising tools providing important information on the determinants of species invasiveness (Moravcová et al. 2010; Suda et al. 2015; Pyšek et al. 2018). Standardised studies on the germination characteristics of plant taxa (Grime et al. 1981, 1988), for example, help clarify the capacity for spreading and the potential for establishment of new populations (Pyšek and Richardson 2007).

In the present study, we describe cytological variability and germination in two newly spreading species, *S. byzantina* and *L. coronaria*. The seeds of both species displayed optimal germination at temperatures between 15/10 and 22/15 °C, with *S. byzantina* closer to 22/15 °C (Figs. 3, 5). Hence both species displayed optimal germination at temperatures, ability and germination in two newly spreading species, which have similar spreading potential but different native ranges, proved highly successful at germinating under temperature conditions typical of Central Europe (Iran, Ireland, and Turkey were only sampled for testing cytological homogeneity). Differing environmental conditions are usually the main reason plants fail to survive or spread in their non-native range (Richardson et al. 1994, 2000; Mack 1996); thus, their ability to germinate successfully in this temperature range allowed them to overcome a major barrier between their native and non-native ranges. Though *L. coronaria* was previously classified as non-invasive in the basic IAS screening study of Moravcová et al. (2010), the species has recently begun spreading, with multiple observations of the species escaping from plantations (Kutlvašr et al. 2019; Vojík et al. 2020). Similarly, *S. byzantina* was originally classified as casual in the study of Pyšek et al. (2012b), but has recently shown similar spreading behaviour as *L. coronaria* in the field (see Online Resource figure).

Germination, and timing of germination, depend heavily on a combination of factors, including light, temperature, and dormancy (Hoyle et al. 2015), with external temperature and available light in particular regulating the enzymes directly involved in germination (Baskin and Baskin 1998). Consequently, these two key factors formed the basis of our study into the germination capabilities of *S. byzantina* and *L. coronaria*.

For *Lychnis coronaria*, a species with extremely high final germination at 22/15 °C (almost 99% of seeds germinated; see Fig. 3), rapid germination within the first six days of the experiment, and a germination rate that does not differ between populations of the species, our results were similar to those of Moravcová et al. (2010). However, we disagree with their suggestion that this species does not display invasive behaviour. The species’ high final germination under conditions typical of its non-native range and its rapid growth both increase its ability to invade new environments (Beerling and Perrins 1993; Gioria et al. 2016), and numerous recent recordings of localised spreading in the field (Vojík et al., in prep.) clearly indicate the high invasive potential of the species. An early and/or rapid germination strategy (Ross and Harper 1972; Gioria and Pyšek 2017) is especially typical for ornamental plants originating from arid or semi-arid environments. Indeed, the same strategy is found in a number of fast-growing invasive annuals, including Himalayan balsam *Impatiens glandulifera*, and some of the most invasive monocarpic perennials, including giant hogweed *Heracleum mantegazzianum* and Chilean rhubarb *Gunnera tinctoria* (Gioria and Osborne 2009, 2013). The potential for *L. coronaria* to spread invasively is also supported by its high seed production, with a two-year-old plant releasing 19 000 seeds on average (counted on plants growing in experimental garden bed). Therefore, *L. coronaria* must be considered as a new and potentially dangerous invasive species in this country.

*Stachys byzantina*, was estimated to show highest germination at around 22/15 °C, similar to related species of dry grasslands *S. germanica* (highest germination 20/15 °C; Dunn 1997). Our results confirmed this expectation, with highest germination (55.6%) indeed occurring at 22/15 °C, while almost no seeds germinated (0.3%) at temperatures <10/5 °C. Furthermore, the two populations examined (SB 1, SB 4) differed from each other—their final germination rate at 22/15 °C was 72.8% and at 15/10 °C was 65.6% (Fig. 4), which is about 30% higher than the germination rate of the rest of the tested populations. The explanation may be an adaptation to human-made habitats in urban areas. Urban environments and phenomena (e.g. urban heat and dry islands) strongly influences species adaptation (Williams et al. 2015; McDonnell and Hahs 2015); species are changing their ecological and reproductive traits to become...
more invasive (Dubois and Cheptou 2017). Such phenomenon has been described in several highly invasive European species, including the highly invasive common ragweed Ambrosia artemisiifolia (Gorton et al. 2018). However, we did not study the influence of maternal population growth conditions on germination and it could be the reason for the described difference among populations of the species, in spite of similar site conditions of maternal plants (described in detail in “Material and Methods”).

The final germination was relatively high and contradicts the expected reproduction limits typical for rare, often endemic, species (Pavlik et al. 1993; Kaye 1999), though these can vary between specific sites (e.g. with altitude) or with the age of the populations sampled (Giménez-Benavides et al. 2005). Until recently, it was believed that a small native range would not include many safe sites for sexual propagules (germination conditions), and that this would limit species from spreading in other part of the world (Massey and Whitson 1980). However, there are now numerous examples of rapid and heavy invasion by such species, e.g. I. glandulifera (Beerling and Per rins 1993), suggesting that a species’ individual ecological characteristics and its ability to evolve may be all that is needed to produce invasive behaviour (Dlugosch and Parker 2008a).

We also analysed the cytological variability of both S. byzantina and L. coronaria to determine differences in ploidy levels among their populations. We did not assess genetic diversity as it was expected to be high in both species due to their predominant generative reproduction mode (Crawley 1996). Nevertheless, genome size variability is a fast screening method for detecting changes in ploidy level or ongoing evolution that can affect seed germination and/or growth rate (Pegtel 1999; Schween et al. 2005; Münzbergová 2006). Polyploidy, for example, can...
cause differently sized seeds, changes in viability, and changes in a species’ ability to germinate under stressful conditions (Stevens et al. 2020). Such changes to genome size can significantly influence the ability of an alien species to spread and potentially become invasive (Suda et al. 2015; Pyšek et al. 2018). Our results indicated that both species were cytologically homogenous with no evidence of polyploidy, with all populations of either species having a similar species-specific genome size (S. byzantina 1.55–1.63 pg; L. coronaria 6.40–6.58 pg), levels similar to those given by Zonneveld (2019). Furthermore, reference samples taken from the species’ native range around Istanbul in Turkey (LC 7) and Tehran in Iran (SB10) showed the same ploidy levels as those from the non-native range (Online Resource table).

Comparison of escaping and non-escaping populations

Based on field observations (visual detection of escapes), we expected to see a difference in cytological variability and final germination between escaping and non-escaping populations. Surprisingly, our results failed to show any significant difference in variability and germination rate for either species examined (see Fig. 5), suggesting that germination and genome size are not key factors for escape from plantations. However, spreading into surrounding habitats could be caused by changes in local site conditions, such as management or disturbance regime (Buckley et al. 2007). Both species have now been recorded escaping from urban habitats, especially parks and gardens (Hejný 1997; Barošová and Baroš 2009; Pergl et al. 2016; Kutlvašr et al. 2019; Vojík et al. 2020). While both species are currently classified as naturalised (L. coronaria) or casual (S. byzantina) (Pyšek et al. 2012b), they are likely to become problematic species as they spread into natural or semi-natural habitats, with rural semi-dry grasslands as well as semi-natural species-rich grasslands and steppes particularly at risk. L. coronaria is a particularly competitive species due to its ability to produce a huge number of viable seeds that can be spread in different ways (e.g. hydrochory, epizoochory), allowing it to spread into faraway habitats (Moravcová et al. 2010). S. byzantina can spread successfully by either seed or vegetative dispersal. It is also likely that S. byzantina could erode the genome of the endangered native species, S. germanica, through hybridisation (see Introduction); this process is generally considered one of the most serious impacts of invasive species on native biota (Largiadèr 2008; Muhlfeld et al. 2014).

Overall, our results suggest that generative spreading of both L. coronaria and S. byzantina is directly influenced by environmental factors, such as mean and spring temperature, both of which are likely to increase due to global climate change (Hansen et al. 2006; Anderson et al. 2008). In addition, indirect phenomena such as dry and warm islands in urban habitats (Roth et al. 1989; Lokoshchenko 2017; Yang et al. 2017; Hao et al. 2018) may be increasing the likelihood of these species escaping and spreading further. As such, both species may now pose a real threat to native species, particularly those in Central European mesic and xeric grasslands.

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