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Source: Ecoscience, 16(2) : 248-257

Published By: Centre d'études nordiques, Université Laval

URL: https://doi.org/10.2980/16-2-3234

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ECOSCIENCE 16 (2): 248-257 (2009)

Germination requirements and seed mass of slow- and fast-colonizing temperate forest herbs along a latitudinal gradient[1]

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Abstract: Predictions on displacement of suitable habitats due to climate change suggest that plant species with poor colonization ability may be unable to move fast enough to match forecasted climate-induced changes in habitat distribution. However, studies on early Holocene plant migration show fast migration of many plant species that are poor colonizers today. We hypothesize that warmer temperatures during the early Holocene yielded higher seed quality, contributing to explaining the fast migration. We studied how the 3 seed quality variables, seed mass, germinability, and requirements for break of seed dormancy, vary for seeds of 11 forest herb species with varying colonization capacity collected along a 1400-km latitudinal gradient. Within species, seed mass showed a positive correlation with latitude, whereas germinability was more positively correlated with temperature (growing degree hours obtained at time of seed collection). Only slow-colonizing species increased germinability with temperature, whereas only fast-colonizing species increased germinability with latitude. These interactions were only detectable when analyzing germinability of the seeds, even though this trait and seed mass were correlated. The requirement for dormancy break did not correlate with latitude or temperature. The results indicate that seed development of slow colonizers may be favoured by a warmer climate, which in turn may be important for their migration capacity.
Keywords: ancient forest, climate change, plant migration, Reid's paradox, seed development, seed dormancy.

Résumé : Les prévisions de déplacement des habitats en fonction du changement climatique suggèrent que les espèces végétales ayant une faible capacité de colonisation puissent être incapables de se déplacer assez rapidement pour suivre les modifications prévues à la distribution des habitats. Cependant, des études de la migration des plantes au début de l'Holocène montrent une migration rapide de plusieurs espèces végétales qui ont aujourd'hui une faible capacité de colonisation. Nous formulons l'hypothèse que les températures plus chaudes du début de l'Holocène ont permis la production de graines de plus grande qualité contribuant à expliquer leur migration rapide. Nous avons étudié comment les 3 variables de qualité de la graine, la masse, le pouvoir germinatif et les exigences de levée de dormance varient pour des graines de 11 espèces herbacées forestières possédant différentes capacités de colonisation récoltées le long d'un gradient latitudinal de 1400 km. Pour une même espèce, la masse de la graine était corrélée de façon positive avec la latitude, alors que le pouvoir germinatif était plus corrélé positivement avec la température (degrés-heures de croissance au moment de la récolte de la graine). Seules les espèces à colonisation lente avaient une augmentation de leur pouvoir germinatif avec la température alors que seules celles à colonisation rapide avaient une augmentation de leur pouvoir germinatif avec la latitude. Ces interactions étaient détectables seulement en analysant le pouvoir germinatif des graines, même si ce trait était corrélé avec la masse de la graine. Les exigences de levée de dormance n'étaient pas corrélées avec la latitude ou la température. Ces résultats indiquent que le développement des graines à colonisation lente peut être favorisé par un climat plus chaud, qui à son tour peut être important pour leur capacité de migration.
Mots-clés : changement climatique, développement de la graine, dormance de la graine, forêt ancienne, migration des plantes, paradoxe de Reid.

Nomenclature: Tutin *et al*., 2001

[1]Rec. 2008-11-05; acc. 2009-04-07.
Associate Editor: Johannes Kollmann.
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DOI 10.2980/16-2-3234

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Introduction

It is well established from paleoecological studies that climatic changes cause displacement of plant distributions. Future global warming is therefore expected to cause large vegetation shifts and long-distance plant migration towards higher latitudes and altitudes (Christensen *et al*., 2007). Plant migration requires good colonization capacity, and there is a growing concern that plant species that in the present landscape demonstrate poor colonization capacity will not be able to track their suitable habitats at a sufficient speed and hence will suffer major decline in distribution area (Honnay *et al*., 2002; Higgins, Lavorel & Revilla, 2003; Skov & Svenning, 2004). Many common herb species growing in temperate forests in Europe and North America are known to have poor colonization capacity in the present landscape (Hermy *et al*., 1999; Flinn & Vellend, 2005). Studying forest herbs that we know vary in colonization capacities may be useful in revealing patterns important for understanding climate impacts on plant distribution both in the past and the future.

Long-distance migration requires successful colonization by seeds for most plant species. The colonization process by seeds requires successful seed production, seed dispersal, break of seed dormancy, germination, and seedling survival to establish new individuals and populations. If any of these processes is limited the species will decrease its colonization capacity (*cf*. Hermy & Verheyen, 2007). The poor colonization capacity of many forest herb species has been ascribed to poor seed dispersal ability (Hermy *et al*., 1999; Graae, 2000; Verheyen *et al*., 2003; Brunet, 2007). Three major arguments have been used: 1) many of the poorly colonizing species lack adaptation to long-distance dispersal (Matlack, 1994; Graae, 2000; 2002; Matlack, 2005), 2) long distances between forest habitats in the temperate agricultural landscape limit colonization (Brunet, von Oheimb & Diekmann, 2000); and 3) seed sowing experiments showed that recruitment often takes place when seeds are added (Eriksson & Ehrlen, 1992; Graae, Hansen & Sunde, 2004; Van der Veken *et al*., 2007). These are all good indications of limited seed dispersal, but there are indications that limited seed dispersal cannot solely account for the poor colonization capacity.

More than one hundred years ago Clement Reid was already wondering how oak could migrate so rapidly during the early Holocene considering its slow spread at present. This question has been termed Reid's Paradox (Clark *et al*., 1998). As the colonization processes in the early Holocene seem to have been much more efficient compared to present observed colonization rates, we may expect that some environmental difference(s) between the past and the present affect the colonization process. Based on the assumed importance of seed dispersal, former higher density of large herbivores may be suggested. However, even species without adaptations to zoochorous dispersal and with poor colonization capacity in the present landscape spread over large distances in Northern Europe during the early Holocene. Furthermore, while isolation in the fragmented landscape seems to limit current colonization, even migration rates within forest stands seem to be very slow (Brunet & von Oheimb, 1998; Bossuyt, Hermy & Deckers, 1999). Hence, more spatial continuity, such as dispersal corridors, would most likely not increase dispersal distances and colonization capacity to that observed in the early Holocene. Finally, the seed sowing experiments carried out with forest herbs demonstrated that when seeds are present some species will recruit, but these experiments also demonstrated notable lack of recruitment in many species, low numbers of recruited seedlings in other species (Eriksson & Ehrlen, 1992; Ehrlén & Eriksson, 2000; Graae, Hansen & Sunde, 2004), and low establishment of viable adult plants and populations (Ehrlen *et al*., 2006; see however Van der Veken *et al*., 2007). As Clark *et al.* (2007) pointed out, recruitment of a few seedlings does not guarantee individual or population establishment and spread. Recruitment limitation can either be ascribed to the number and quality of the seeds or the microsites. Studies on soil variables in occupied and non-occupied forest stands have tested whether poor colonization capacity could be due to microsite quality and have found little support for this explanation (Graae, Sunde & Fritzbøger, 2003; Verheyen *et al*., 2003).

As the climate in the early Holocene was warmer than today and climate is known to affect reproduction of many species, we suggest acknowledging that climate affects not only the distribution of habitats but also the intrinsic colonization capacity of forest herbs (Ibanez *et al*., 2007).

Few studies have tested the impact of climate on reproduction of forest herb species, despite the fact that laboratory studies have demonstrated that several processes in the reproductive pathway are temperature related (Baskin & Baskin, 1998; Gutterman, 2000; Probert, 2000; Finch-Savage & Leubner-Metzger, 2006). If climate is an important variable in colonization capacity, climate change may contribute to explaining Reid's Paradox; it is also important to incorporate the impact of climate on recruitment processes of field species when modeling plant distribution in future warmer climates.

In the present study we focus on the first element in the colonization process expected to relate to climate: seed formation. Seed formation results in seeds of varying quality, which can be measured as the germination percentage of the seeds. Germination percentages are time consuming to obtain, however, and it is not always known how to treat the seeds to get the highest germination percentage. Therefore, an easier measurable trait reflecting germination percentage would be convenient as a surrogate trait. Seed mass could be used as such a soft trait (*sensu* Jeltsch *et al*., 2008) if germination percentage and seed mass correlate closely. From a climate change perspective, the germination percentage obtained under optimal temperature treatment is relevant, but the climatic requirements for breaking seed dormancy are crucial. Many forest species have demanding requirements for break of seed dormancy and low germination percentages when tested in incubators (Grime *et al*., 1981), and Verheyen *et al*. (2003) demonstrated that slow-colonizing species have more restrictive germination requirements than fast-colonizing ones. As the requirements for break of seed dormancy vary with the environment affecting the maternal plant during seed formation (Baskin & Baskin, 1998; Cavieres & Arroyo, 2000; Ellison, 2001), we looked at this trait as a third seed quality measure.

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In this study, we investigate how germination percentage, seed mass, and dormancy-breaking requirements change for seeds collected along a 1400-km-long latitudinal (10°) gradient from northern France to central Sweden. Mean annual temperature decreases 3.7 °C from north to south along this transect, thereby presenting a clear climatic gradient. Using a set of 11 long-lived forest herbs that according to literature differ in their colonization abilities, we specifically explored the following:

A. Do seeds of poor colonizers have low seed mass, low germinability, and/or demanding requirements for break of dormancy?

B. Do seeds of poor colonizers increase seed quality with temperature during seed formation?

C. Does seed mass reflect germinability, and is it suitable as a soft trait in climate impact models of population dynamics and vegetation changes?

Methods

STUDY SPECIES

Eleven herbaceous species common in closed forests and representing a broad range of colonization abilities were selected for this study: *Anemone nemorosa*, *Lamiastrum galeobdolon*, *Melica uniflora*, *Mercurialis perennis*, *Oxalis acetosella*, *Stachys sylvatica*, *Stellaria holostea*, *Brachypodium sylvaticum*, *Carex sylvatica*, *Circaea lutetiana*, and *Geum urbanum*. All are common in northwestern and central Europe. The first 7 have adaptations to dispersal by ants or do not have any attachments that aid dispersal, while *Brachypodium sylvaticum*, *Carex sylvatica*, and especially *Circaea lutetiana* and *Geum urbanum* possess structures for epizoochorous seed dispersal (Hodgson *et al*., 1995).

Seeds of *Brachypodium sylvaticum*, *Carex sylvatica*, *Geum urbanum*, *Lamiastrum galeobdolon*, *Mercurialis perennis*, *Oxalis acetosella*, and *Stachys sylvatica* have physiological dormancy, whereas *Anemone nemorosa* seeds have morphophysiological dormancy, in which both growth of the embryo and break of the physiological inhibiting mechanism are needed before germination can occur (Baskin & Baskin, 1998). We found no information on dormancy in seeds of *Circaea lutetiana*, *Melica uniflora*, and *Stellaria holostea*, but other members of these genera have physiological dormancy (Baskin & Baskin, 1998).

For each species, a colonization capacity index (CCI) was calculated following Verheyen *et al*. (2003). In addition to data from the studies in Verheyen *et al*. (2003), data from 7 recent publications (Heinken, 1998; Graae, 2000; Graae & Sunde, 2000; Jacquemyn, Butaye & Hermy, 2001; Wulf, 2003; Brunet, 2004; Kolb & Diekmann, 2004) were used in the calculation of the CCI. The data met the same criteria as given in Verheyen *et al*. (2003), and the same methods were used for calculating the CCI (but with opposite sign, *cf*. Hermy & Verheyen, 2007). The formula therefore becomes

$$\mathrm{CCI} = \frac{(\{1.5 \times \mathrm{R}^* + \mathrm{R}\} - \{1.5 \times \mathrm{A}^* + \mathrm{A}\})}{(\mathrm{A}^* + \mathrm{A} + \mathrm{R}^* + \mathrm{R})} \times \frac{100}{1.5} \qquad [1]$$

where R* is the number of studies in which species X is significantly more frequent in recent forest; R is the number of studies in which species X is equally frequent or tends to be more frequent in recent forest; A* represents the number of studies in which species X is significantly more frequent in ancient forest; and A is the number of studies in which species X is more frequent, but not statistically significant, in ancient forest. For studies lacking statistical analyses of species affinity with ancient forest, we calculated Pearson Chi^2 association measures. The index ranges from 100 (strongly associated with recent forest) to –100 (strongly associated with ancient forest). CCI varied from 29 to –84. *Geum urbanum* is the best colonizer (having the positive value), while the other species have values between –15 and –84 (Appendix I).

SEED COLLECTION

Whole diaspores were used and are referred to as seeds throughout the rest of the paper. Mature seeds were collected during 2005 in 6 lowland regions distributed along an approximately 1400-km-long SW–NE transect from northern France to central Sweden (Appendix I). In each of the regions—northern France, Belgium, northwestern Germany, northeastern Germany, southern Sweden and central Sweden—1 site for each study species was chosen in closed-canopy forest on level ground, typical for the species and with as large a population as possible to avoid possible negative demographic effects on seed characteristics (*e.g*., due to low genetic diversity or decreased pollination in small populations). In total, 62 seed samples were used for the 11 species and the 6 sites (not all species could be collected in all regions). The seeds were air dried for a few days at room temperature and subsequently sent to the Climate Impacts Research Centre in northern Sweden for further processing.

GERMINATION TESTS AND SEED MASS DETERMINATION

For each seed sample, 6 Petri dishes were lined with moist filter paper (Munktell 00A) and 25–50 seeds (depending on number of seeds available) were distributed in each dish for the germination trials as soon as possible after collection (most samples within 2 weeks). Petri dishes were placed in plastic bags to avoid desiccation during incubation. Three dishes were placed directly in warm incubation at a light and temperature regime of 14 h light (240 $\mu mol \cdot m^{-2}s^{-1}$)/20 °C and 10 h dark/10 °C. The number of germinated seedlings was recorded every 2 weeks. After 6 weeks the dishes were moved to cold stratification (2 °C and darkness), where they were kept for 18 weeks. After this cold stratification, the Petri dishes were transferred to warm incubation for another 6 weeks (same light and temperature regime as above), with recordings again taken every 2 weeks. Data obtained from these 3 dishes per seed sample resulted in 2 sets of germination percentages: 1) warm incubation (W): germination of fresh seeds; and 2) warm+cold+warm incubation (WCW): combined germination of both the fresh seeds and the additional germination during stratification and the second round of warm incubation. The remaining 3 dishes from each seed sample were directly cold stratified for 18 weeks and then transferred to warm incubation for 6 weeks (same light and

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temperature regime as above). The number of seeds germinated during this trial gave rise to a third set of germination percentages: 3) cold+warm incubation (CW): germination of cold-stratified seeds. The germinability of the seeds is defined as the maximum germination percentage of seeds that were obtained in any of the 2 sets of Petri dishes (CW or WCW)

For each seed sample, 50 additional seeds were air dried at room temperature for a minimum of 30 d and the seeds weighed one by one.

Temperature data

Weather data from 2005 were included in the analysis by calculating the number of growing-degree hours (GDH) above 5 °C between January 1, 2005 and the species-specific seed collection dates. GDH is a widely used heuristic tool in phenology that has many applications in, *e.g.*, agriculture as it has been shown to correlate well with plant development (*e.g.*, Larcher, 2003; Finch-Savage & Leubner-Metzger, 2006). Calculations were done according to Lindsey and Newman (1956) using daily minimum and maximum temperatures from weather stations in Amiens (northern France), Bevekom (Belgium), Bremen (NW Germany), Potsdam (NE Germany), Lund (southern Sweden), and Stockholm (central Sweden), all as close as possible to the seed collection sites.

Data analysis

An Immediate Germination Index (IGI) was constructed as follows:

$$\text{IGI} = \frac{(3(\text{W}) + 2(\text{CW}) + 1(\text{WCW} - \text{W}))}{\text{Germinability}} \quad [2]$$

where W is the germination percentage of fresh seeds, CW is the germination percentage after cold stratification followed by warm incubation, and WCW is the germination percentage after warm incubation followed by cold stratification and warm incubation (W is subtracted to exclude the seeds germinated as fresh seeds). Hence, a high IGI indicates high germination percentage without any stratification treatment, and a low value indicates that most seeds needed both warm and cold stratification before germination occurred.

For the among-species analyses, mean values for the seed quality variables of each of the 11 species across all samples were calculated. As the number of species was low and data were not normally distributed, Spearman Rank correlations were used to test for relationships between the CCI, seed mass, germinability, and the IGI.

To test for effects of climate and latitude on seed mass within species, a General Linear Model (GLM) was applied. Therefore, GDH and latitude were included as covariates, and possible differences in effects of GDH and latitude between faster- and slower-colonizing species were tested through inclusion of the interactions with the factor colonization group. The random factor colonization group was defined to have 2 levels, slow-colonizing species (CCI < –50; 6 species) and faster-colonizing species (CCI > –50, 5 species). To allow a joint statistical analysis of species, seed mass values were standardized for each species by dividing each individual seed mass by the mean seed mass of that species across all sites. Similarly, GDHs were standardized per species by dividing site-specific values by the overall mean to be able to compare differences in GDHs over all sites and all species. Finally, $\log_2$+1-transformation of the seed mass was necessary to meet the statistical assumptions.

To test for effects of climate and latitude on germinability, a similar GLM was performed on the $\log_2$+1-transformed standardized germinability (*cf.* above). To test whether patterns in germinability were caused by correlation with seed mass, a third model was run, but with seed mass included as a covariate.

The effects of climate and latitude on the requirements to break dormancy were again tested using a similar GLM, but this time with IGI as response variable.

Appendix I shows all data obtained in the experiment and used in the data analysis listed for the species in the order of increasing colonization index CCI. Due to a shortage of seeds and a mistake in the laboratory procedures during the germination trials the resulting sample size was decreased slightly in the different analyses. All analyses were performed with SPSS 15.0.

Results

In the among-species analyses, the CCI was not significantly correlated with any of the seed quality measures ($r_s < 0.45$, $P > 0.17$, $n = 11$ for all 3 variables). Germinability decreased significantly with seed mass ($r_s = –0.75$, $P < 0.01$, $n = 11$) and increased with IGI ($r_s = 0.66$, $P < 0.05$, $n = 11$), whereas the correlation between IGI and seed mass was only marginally significant ($r_s = –0.53$, $P = 0.10$, $n = 11$). Hence, large-seeded species tended to have lower germinability and stronger requirements to break dormancy.

Standardized seed mass within species increased significantly by latitude but not significantly by standardized GDH (Table I). Interactions with CCI groups were not significant. Standardized germinability was marginally significantly correlated with latitude and standardized GDH (Table II). Interactions between the CCI groups and both the standardized GDH and latitude were significant. Only the slow-colonizing species increased standardized germinability significantly with standardized GDH ($R^2 = 0.17$, $P = 0.016$, see Figure 1a). The back-transformed germination percentage indicates that an increase in the GDH of 20% increased the germination percentage by 30 to 33% for the group of slow-colonizing species. Only the fast-colonizing species increased standardized germinability with latitude ($R^2 = 0.14$, $P = 0.049$, see Figure 1b). The back-transformed germination percentage indicates that an increase in latitude of 1° increased the germination percentage by 6 to 9% for the group of better-colonizing species.

Standardized seed mass and germinability were significantly positively correlated ($r = 0.35$, $P < 0.01$, $n = 61$), with the variability in seed mass (range 40–160% of the average mass) being smaller than the variability in germinability (range ~0–300% of the average germination percentage). If the GLM

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is run with standardized germinability as dependent variable and standardized seed mass included as explanatory variable, standardized seed mass also explains a significant part of the variation ($F_{1, 53} = 5.80$, $P < 0.05$), leaving the latitude ($F_{1, 53} = 1.87$, $P = 0.18$) and GDH ($F_{1, 53} = 1.68$, $P = 0.2$) insignificant in the model, whereas the interactions with CCI remain significant in the model ($F_{1, 53} = 4.58$ and 4.48 for standardized GDH and latitude, respectively, and $P < 0.05$ for both).

There was no impact of latitude or standardized GDH on dormancy breaking requirements (Table III).

Discussion

In the present study, slow colonizers did not have particularly poor germinability or complicated break of dormancy patterns compared to fast colonizers, but the results demonstrated that the slow-colonizing species increased their number of germinable seeds when growing in a warmer climate. In contrast, the better colonizers increased their germinability with latitude rather than with temperature. Although germinability was correlated with seed mass within species, germinability seemed more strongly affected by temperature than seed mass did. The implications of these results are discussed below.

The small number of species in the present study obviously limited the chances of observing interspecific differences. We saw no significant pattern of poor colonizers having low germinability compared to that of the faster colonizers. However, large-seeded species tended to have lower germinability and stronger requirements to break dormancy. Large seed size has been demonstrated to be associated with poor colonization capacity in forest herb species (Graae,

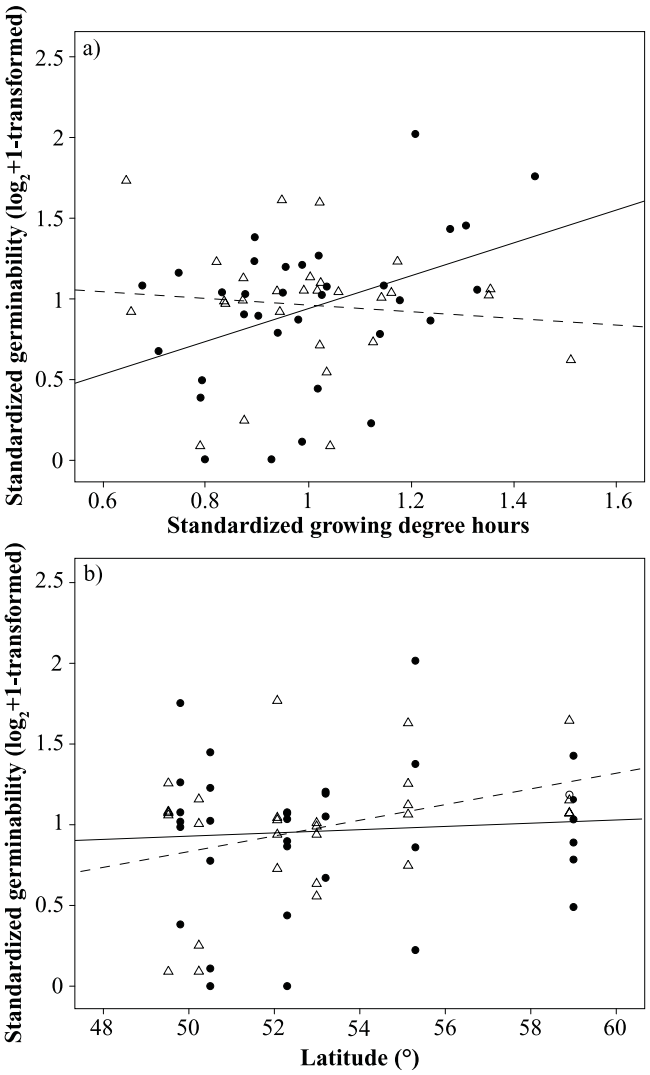

FIGURE 1. Relationships between the $\log_2$+1-transformed standardized germinability and a) the standardized growing degree hours and b) the latitude for both the slow-colonizing species (filled circles, full line; $R^2_a = 0.17$ and $R^2_b = 0.01$) and the fast-colonizing species (empty triangles, dashed line; $R^2_a = 0.01$ and $R^2_b = 0.14$).

TABLE I. Results of the GLM analysis with the $\log_2$+1-transformed standardized seed mass as response variable and latitude, the standardized growing degree hours (Stand. GDH), and their interactions with the colonization group (2 levels: slow- and fast-colonizing species) as explanatory variables ($n = 60$; $R^2 = 0.09$).

Variable	*F*-value	*P*-value	Effect size*
Stand. GDH	$F_{1, 55} = 2.40$	0.13	0.04
Latitude	$F_{1, 55} = 4.13$	**0.05**	0.07
Stand. GDH × Colonization group	$F_{1, 55} = 0.02$	0.89	< 0.01
Latitude × Colonization group	$F_{1, 55} = 0.01$	0.93	< 0.01

*Partial Eta squared: ratio of the variation accounted for by the variable to the sum of the variation accounted for by the variable and the variation unaccounted for by the model as a whole.

TABLE II. Results of the GLM analysis with the $\log_2$+1-transformed standardized germinability as response variable and latitude, the standardized growing degree hours (Stand. GDH), and their interactions with the colonization group (2 levels: slow- and faster-colonizing species) as explanatory variables ($n = 61$; $R^2 = 0.17$).

Variable	*F*-value	*P*-value	Effect size*
Stand. GDH	$F_{1, 56} = 3.16$	0.08	0.05
Latitude	$F_{1, 56} = 3.86$	**0.05**	0.06
Stand. GDH × Colonization group	$F_{1, 56} = 5.70$	**0.02**	0.09
Latitude × Colonization group	$F_{1, 56} = 5.70$	**0.02**	0.09

*Partial Eta squared: ratio of the variation accounted for by the variable to the sum of the variation accounted for by the variable and the variation unaccounted for by the model as a whole.

TABLE III. Results of the GLM analysis with the immediate germination index (IGI) as response variable and latitude, the standardized growing degree hours (Stand. GDH), and their interactions with the colonization group (2 levels: slow- and fast-colonizing species) as explanatory variables ($n = 59$; $R^2 = 0.09$).

Variable	*F*-value	*P*-value	Effect size*
Stand. GDH	$F_{1, 54} = 0.00$	0.99	< 0.01
Latitude	$F_{1, 54} = 0.95$	0.33	0.02
Stand. GDH × Colonization group	$F_{1, 54} = 0.02$	0.89	< 0.01
Latitude × Colonization group	$F_{1, 54} = 0.08$	0.77	< 0.01

*Partial Eta squared: ratio of the variation accounted for by the variable to the sum of the variation accounted for by the variable and the variation unaccounted for by the model as a whole.

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Hansen & Sunde, 2004), and poor colonizers among forest species have been demonstrated to have higher requirements to break of dormancy (Verheyen *et al*., 2003). Our results do not support these findings, but we suggest that studies with more species to be carried out to reveal the interspecific patterns of reproductive capacity of poor compared to fast colonizers.

Analyzing the intraspecific variations in all species, latitude was more important for seed mass than temperature was. For many species, seed mass decreases with latitude (Moles & Westoby, 2003), but we found a positive correlation between seed mass and latitude within the species. The many variables that have been demonstrated to correlate with latitude (Jansson & Davies, 2007; Moles *et al*., 2007) leave various options for interpretation of the results. Seed mass may be determined by the environment during seed development. One may argue that colder temperatures towards the poles mean shorter time for seed development, and hence smaller seeds, compared to lower latitudes. On the other hand, seeds are set later at higher than at lower latitudes, and the increased light regime during the time of their development may be more important than temperature and the length of the growing season for seed development. Increased seed mass with increased latitude may also be related to selective forces such as requirements for rapid seedling establishment in less favourable climates with shorter growth seasons. Increased seed mass for species in increasingly physiologically stressful environments has also been reported by Caddick and Linder (2002).

The most intriguing result of the present study was that slow-colonizing species increased their germinability with warmer climate. This was unrelated to the effect of latitudinal gradient on seed size. These results indicate that species that are today's poor colonizers could become better colonizers in warmer climates, because increased germinability may favour recruitment ability of their seeds. This result also adds interesting aspects to the old debate on how species that are today poor colonizers showed fast migration in the early Holocene. An increased recruitment rate in the warmer early Holocene climate (Kullman, 1998) through increased germination may have added to the fast population spread (Ibanez *et al*., 2007). The relative importance of such processes for migration rates of slow colonizers has yet to be tested.

Another very interesting pattern in the data was that fast colonizers showed significantly increased germinability with latitude, whereas no such trend was obvious for the slow colonizers. As this pattern was not caused by the GDH, other variables related to latitude may drive the pattern. The observed pattern could be related to the increasing day length during seed set or to the openness of forest canopy where the species occur, which also may increase with latitude. The fast-colonizing species (*Geum urbanum, Brachypodium sylvaticum, Mercurialis perennis, Stachys sylvatica*, and *Circaea lutetiana*) differ from the slow colonizers in several ways. Most of the fast-colonizing species have late seed set, and they are often found in more open forests compared to slow colonizers (*Anemone nemorosa, Oxalis acetosella, Lamiastrum galeobdolon, Melica uniflora, Stellaria holostea,* and *Carex sylvatica*). Perhaps the fast-colonizing species are more favoured by or dependent on long days with plenty of light for seed development compared to the slow ones, which are adapted to early seed set where at least part of the flowering is before the canopy closes.

When evaluating intraspecific differences we found that low seed size for a species is associated with low germinability. This supports the notion that seed size can be used as a good soft trait for germinability. On the other hand, the relationships between germinability on the one side and GDH and latitude on the other did not change when seed mass was entered as covariate. This indicates that although seed mass and germinability were correlated, the patterns in germinability with respect to colonization capacity could only be revealed by evaluating germination of the seeds. Hence, studies on germinability of seeds may reveal information not revealed in studies where only seed mass is analyzed, and there is certainly a need to know more about the relationship between seed mass and germinability if we are to use seed mass as a valuable soft trait in analyses, such as migration and population expansion modelling.

Numerous other climate-related variables are important to reproductive success in addition to seed formation. Density of established vegetation, herbivory, litter depth, soil nutrients, and microclimate during dormancy breaking, germination, and seedling recruitment may affect seedling emergence. There is an urgent need to increase our knowledge of climate impacts on recruitment processes to understand migration processes of different plant functional types.

Acknowledgements

We want to thank J. Ehrlén for help in collecting seeds and A. Moles and O. Eriksson for suggesting valuable improvements to the manuscript. This study was made possible thanks to the Scientific Research Network "FLEUR", funded by the Research Foundation – Flanders (FWO).

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APPENDIX I. Positions for each population of sampled species and Colonization Capacity Index value (CCI), sampling dates (Julian date is day number after January 1st), and seed mass, as well as the mean germination percentage and standard deviation for all seed samples. Fresh (W) denotes seeds germinated within 2 weeks after sampling, CW gives germination percentage after 18 weeks of cold stratification followed by 6 weeks of warm incubation, and WCW after 6 weeks of warm incubation followed by 18 weeks of cold incubation and 6 weeks of warm incubation. The resulting Immediate Germination Index (IGI) value is given in the last column. Species are ordered with increasing colonization capacity. *Carex sylvatica* was sampled in NE Germany at 2 different sampling times, but gave rather similar results.

Collection site	Latitude	Longitude	CCI	GDH	Seed sample julian date	Seed mass (mg)		Mean germination percentage						
								Fresh (W)		CW		WCW		
						Mean	SD	Mean	SD	Mean	SD	Mean	SD	IGI
Oxalis acetosella														
France	49° 36'	2° 91'	–84	14 537	144	1.2	0.3	0	0	100	0	99	2	3.0
Belgium	50° 58'	3° 48'	–84	12 748	146	1.0	0.3	0	0	96	4	24	18	2.3
NW Germany	53° 11'	8° 40'	–84	14 077	167	0.9	0.2	0	0	49	10	93	7	2.1
NE Germany	52° 17'	13° 07'	–84	14 761	162	1.0	0.3	0	0	79	8	33	16	2.4
S Sweden	56° 24'	12° 58'	–84	15 994	179	0.9	0.3	0	0	9	1	12	3	2.5
C Sweden	58° 55'	17° 10'	–84	13 398	176	0.9	0.4	0	0	2	2	52	33	1.1
Mean				14 253	162	1.0		0		56		52		2.2
Lamiastrum galeobdolon														
France	49° 86'	2° 48'	–84	20 081	164	2.1	1.1	0	0	25	9	14	7	2.6
Belgium	50° 58'	3° 48'	–84	25 583	187	1.5	0.3	0	0	43	2	42	17	3.0
NE Germany	52° 35'	13° 01'	–84	17 112	170	2.0	0.7	0	0	15	12	21	6	2.4
C Sweden	59° 19'	17° 53'	–84	15 508	183	2.2	0.5	0	0	3	3	10	2	1.6
Mean				19 571	176	2.2		0		21		22		2.4
Anemone nemorosa														
France	49° 83'	2° 16'	–83	14 285	143	2.7	0.9	0	0	0	0	40	35	1.0
Belgium	50° 58'	3° 48'	–83	9785	131	2.3	0.8	0	0	0	0	1	2	1.0
NW Germany	53° 19'	9° 23'	–83	7011	125	1.7	0.5	0	0	0	0	10	3	1.0
NE Germany	52° 17'	13° 07'	–83	10 088	143	1.6	0.7	0	0	0	0	6	2	1.0
S Sweden	55° 32'	13° 11'	–83	8871	150	1.9	0.6	0	0	0	0	27	25	1.0
C Sweden	59° 22'	18° 03'	–83	9413	164	2.0	0.7	0	0	0	0	18	14	1.0
Mean				9909	143	2.0		0		0		17		1.0
Melica uniflora														
France	49° 82'	2° 16'	–63	14 285	143	2.1	0.5	0	0	2	2	0	0	2.0
Belgium	50° 48'	4° 42'	–63	16 787	163	3.0	0.6	0	0	0	0	0	0	
NE Germany	52° 35'	13° 01'	–63	14 440	160	3.3	0.6	0	0	0	0	0	0	
S Sweden	55° 33'	13° 18'	–63	21 864	195	4.9	0.7	0	0	3	1	20	7	1.3
C Sweden	58° 57'	17° 36'	–63	23 093	204	3.0	0.8	0	0	3	6	11	7	1.6
Mean				18 094	173	3.3		0		2		6		1.6
Stellaria holostea														
France	49° 83'	2° 16'	–60	17 357	153	2.6	0.7	1	1	33	8	58	6	2.2
Belgium	50° 48'	4° 42'	–60	16 787	163	2.8	0.4	9	5	3	6	42	4	1.6
NW Germany	53° 11'	8° 40'	–60	14 077	167	2.5	0.6	4	0	13	10	72	16	1.5
NE Germany	52° 35'	13° 01'	–60	14 440	160	2.6	0.8	19	8	11	2	49	5	2.2
C Sweden	59° 19'	17° 53'	–60	11 003	169	2.5	0.9	58	2	23	1	73	8	3.2
Mean	14 733	162	2.6	18	17	59								2.1
Carex sylvatica														
France	49° 31'	2° 89'	–54	29 033	188	1.7	0.4	4	2	96	2	98	0	3.0
Belgium	50° 48'	4° 42'	–54	22 191	177	1.1	0.4	0	0	51	5	91	1	2.1
NW Germany	53° 19'	9° 23'	–54	33 643	234	1.4	0.2	1	1	87	5	95	3	2.9
NE Germany	53° 01'	13° 54'	–54	17 112	170	1.8	0.4	0	1	81	4	96	3	2.7
				+21 046	+181									+2.8
S Sweden	55° 32'	13° 16'	–54	31 337	227	1.7	0.8	3	2	57	4	72	2	2.7
C Sweden	59° 20'	18° 10'	–54	22 838	203	1.9	0.4	0	0	49	9	75	6	2.3
Mean				25 314	197	1.6		2		70		88		2.6
Mercurialis perennis														
France	49° 86'	2° 48'	–36	16 313	149	7.9	3.8	0	0	0	0	1	1	1.0
Belgium	50° 58'	3° 48'	–36	12 344	145	9.1	2.7	0	0	0	0	1	1	1.0
NW Germany	53° 25'	9° 23'	–36	23 658	197	6.1	3.1	0	0	0	0	6	7	1.0
NE Germany	52°17'	13° 07'	–36	10 088	143	9.3	2.5	0	0	0	0	26	16	1.0
S Sweden	56º 24'	12° 58'	–36	15 994	179	7.2	3.4	0	0	0	0	23	8	1.0

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APPENDIX I. Continued.

Collection site	Latitude	Longitude	CCI	GDH	Seed sample julian date	Seed mass (mg)		Mean germination percentage						IGI
								Fresh (W)		CW		WCW		
						Mean	SD	Mean	SD	Mean	SD	Mean	SD	
C Sweden	59° 19'	17° 53'	–36	15 508	184	7.4	3.2	0	0	1	1	12	21	1.2
Mean				15 651	166	7.9		0		0		11		1.0
Stachys sylvatica														
France	49° 31'	2° 89'	–36	29 033	188	1.2	0.3	18	7	39	5	81	1	2.4
Belgium	50° 58'	3° 48'	–36	28 636	196	1.3	0.3	2	3	13	4	91	1	1.3
NW Germany	53° 24'	9° 22'	–36	23 906	233	1.2	0.4	7	5	54	5	73	8	2.7
NE Germany	52° 35'	13° 01'	–36	32 600	216	1.4	0.4	19	9	54	12	77	3	2.9
S Sweden	55° 33'	13° 11'	–36	32 139	230	1.4	0.1	0	0	15	1	50	5	1.6
C Sweden	58° 57'	17° 36'	–36	24 918	210	1.8	0.3	8	0	53	10	90	3	2.4
Mean				28 539	212		1.4	9		38		77		2.2
Circaea lutetiana														
France	49° 82'	2° 16'	–25	53 057	258	2.3	0.9	0	0	32	27	81	6	1.8
Belgium	50° 48'	4° 42'	–25	36 448	222	1.1	0.5	0	0	3	1			
NW Germany	53° 13'	8° 38'	–25	34 140	236	1.7	0.8	4	4	39	11	73	17	2.2
NE Germany	52° 35'	13° 00'	–25	21 046	242	1.5	0.5	0	0	47	6	32	17	2.7
S Sweden	55° 32'	13° 10'	–25	32 139	230	2.4	1	0	0	42	14	102	2	1.8
Mean				35 366	238	1.8		1		33		72		2.1
Brachypodium sylvaticum														
France	49° 82'	2° 16'	–15	49 745	249	2.8	1.7	56	12	51	3	60	11	4.6
Belgium	50° 48'	4° 42'	–15	37 072	255	1.5	0.7	3	3	4	2	8	5	2.8
NW Germany	53° 24'	9° 22'	–15	43 891	275	1.3	0.6	0	0	21	12	16	12	2.8
NE Germany	52° 35'	13° 00'	–15	40 020	272	2.2	1.3	1	2	29	9	39	9	2.5
S Sweden	56° 09'	13° 36'	–15	43 398	272	0	0	51	11	35	17	2.7		
C Sweden	59° 19'	17° 53'	–15	40 186	267	3.6	1.2	0	0	91	8	79	13	2.9
Mean				42 385	265	2.3		10		41		40		3.0
Geum urbanum														
France	49° 82'	2° 16'	29	34 397	202	2.4	0.4	96	0	91	10	96	0	4.9
Belgium	50° 48'	4° 42'	29	24 740	184	0.7	0.2	89	1	82	2	89	1	4.8
NW Germany	53° 11'	8° 40'	29	19 368	184	1.0	0.2	81	4	59	10	81	4	4.5
NE Germany	52° 35'	13° 00'	29	40 020	242	2.1	0.7	94	4	77	6	94	4	4.6
S Sweden	55° 32'	13° 16'	29	31 337	230	2.4	0.7	96	2	39	11	97	1	3.8
C Sweden	58° 57'	17° 36'	29	27 796	220	2.4	0.8	93	4	51	6	97	3	4.0
Mean				29 610	210	1.8		92		67		92		4.4

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