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Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*

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Summary

1 Most experimental populations of perennial forest herbs have been monitored for only a few years and thus only apply to germination and early seedling survival. Moreover, there is a lack of long-term, quantitative data on the rates of spread of populations.

2 We report the results of a cross-range-edge transplant experiment established in 1960 with the perennial forest herb *Hyacinthoides non-scripta*. We evaluated determinants of survival/extinction, performance and migration distances and patterns of 27 transplanted populations after a period of 45 growing seasons.

3 Of 27 experimental populations of *Hyacinthoides non-scripta* implanted in 1960, 11 (41%) were still found in 2005–06. Population survival was independent of soil type and changes in the vegetation layer. In contrast, physical disturbance of the soil and major changes in the tree layer as a result of forest management were the main determinants of population extinction. Current population surface areas ranged from 0.23 to 26.23 m^2. Plant height, leaf length, number of flowers and seed size were generally lower in the introduced populations than in the source populations. However, densities and proportions of non-flowering adults were higher, especially in the larger populations. This suggests that these populations are still expanding with more but younger, and thus smaller, individuals.

4 Observed migration rates were very low, ranging from 0.006 my^{-1} to 0.06 my^{-1}. Migration occurred by the establishment of isolated individuals, which were later absorbed by the advancing wave of the main population. The spread projected for the largest population in the next 45 years is only 14 m for the main population front and 42 m for the furthest individual.

5 Our results may be representative of population spread for slow dispersing forest plant species after occasional long-distance dispersal events across a range edge. However, the slow rates of spread indicate that, even if such events occur, it can take a very long time to establish viable population sizes.

Key-words: dispersal limitation, *Hyacinthoides non-scripta*, migration distance, plant performance, range edge, transplant experiment

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Introduction

The distribution of plant species depends on the availability of suitable habitats, the capacity of plants to disperse to these habitats, and the capacity to establish and persist (Ehrlén & Eriksson 2000; Gaston 2003). When a species is unable to disperse to a suitable habitat, and thus will not occupy all suitable habitat patches at a given time, it is dispersal limited (Primack & Miao 1992; Eriksson 1998). Introductions of diaspores, seedlings or adults are direct ways to identify dispersal limitation in unoccupied habitat patches, and several recent experimental studies have shown that distributions

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of many plant species are indeed dispersal limited on both local (e.g. Turnbull *et al.* 2000; Gustafsson *et al.* 2002; Verheyen & Hermy 2004) and larger geographical scales (Primack & Miao 1992; Ehrlén & Eriksson 1996; Eriksson 1998). However, even when studying perennial plants, most dispersal limitation experiments have only been monitored for a few years and thus often only record germination and early seedling survival. Nevertheless, several studies have stressed the importance of establishment conditions compared with germination (Turnbull *et al.* 2000; Graae *et al.* 2004). Recruitment studies performed during too short a time period may overestimate patch suitability because populations may not be able to persist several years after introduction (Ehrlén & Eriksson 2000). Ehrlén & Eriksson (2000) demonstrated in a seed sowing experiment with seven forest plant species in Sweden that seedlings did not survive for 3 years in almost half of the patches where they had emerged in the first year. Gustafsson *et al.* (2002), who monitored a perennial forest herb transplant experiment for 7 years, showed that the importance of local abiotic factors was only expressed several years after transplantation. Graae *et al.* (2004) sowed eight forest plant species in both ancient and recent forests, and for all species, correlations with soil factors were stronger in the establishment stage compared with the recruitment stage. It was suggested that recording of transplant data should be extended from 1 or 2 years to longer periods in order to have better estimates of true dispersal and recruitment limitation in perennial plants (Turnbull *et al.* 2000; Gustaffson *et al.* 2002; Graae *et al.* 2004).

Another disadvantage of short-term experiments is the lack of quantitative data on the rates of spread of the transplanted populations. To date, very few studies have quantified migration rates of perennial woodland herbs, and most of these have studied invasion into newly established forests next to ancient forests (Matlack 1994; Brunet & Von Oheimb 1998; Bossuyt *et al.* 1999; Honnay *et al.* 1999; Dzwonko 2001; Verheyen & Hermy 2001). Primack & Miao (1992) and Heinken (2004) have studied annual species experimentally for several generations but it is not known whether the results they obtained are relevant for perennial plants. Petersen & Philipp (2001) transplanted 37 woodland herbs, most of which were perennials, into a recently established forest stand and monitored species survival and spread for 10 years. Most species performed badly or even disappeared within 6.5 years.

In this study, we report the results of a transplant experiment established in 1960 to implant experimental populations of *Hyacinthoides non-scripta* into a forest situated outside its current range. After rediscovering detailed field notes of this experiment, the forest was revisited to evaluate the performance of the transplanted populations after 45 growing seasons, and to compare the performance of *H. non-scripta* in these transplanted populations and in the three source populations. We adopted a methodology proposed by Caughley *et al.* (1988) (and reviewed by Hoffmann & Blows 1994) that involves measuring three characteristics of both source and introduced populations: the rate of increase, density within populations and the performance of the individuals. Further, migration distances and patterns were quantified. More specifically, the following questions were addressed (cf. Ehrlén & Eriksson 2000). (i) Is the regional distribution of *Hyacinthoides non-scripta* limited by dispersal? (ii) Can sites with extant populations be distinguished from those with extinct populations by habitat characteristics such as soil chemistry, vegetation composition or forest management? (iii) How do the introduced populations perform in comparison with the source populations? (iv) What type of colonization rates and patterns are found in the spreading populations? As the studied populations were implanted just outside the current range of the species, our results may be representative of establishing and spreading plant populations after occasional long-distance dispersal events across a range edge. In the current context of climate changes and habitat fragmentation, this might be the only way species can expand their ranges in the future (Cain *et al.* 1998; Honnay *et al.* 2002; Nathan 2006).

Materials and methods

The study was performed near the city of Liège in Belgium, *c.* 80 km east-south-east of Brussels, in the Vecquée forest, an ancient public forest that spans an area of 730 hectares (Fig. 1). Height above sea level is approximately 270 m and local topography is determined by small rivulets crossing the forest. The soils are sandy to loamy and generally well drained. The tree layer consists of a mixture of deciduous species, mainly consisting of *Quercus robur*, *Q. petraea* and *Fagus sylvatica*, and a ground layer with diverse herbaceous vegetation (main spp. *Pteridium aquilinum*, *Atyrium filix-femina*, *Millium effusum* and *Luzula luzuloides*).

Hyacinthoides non-scripta (L.) Chouard is a perennial forest herb confined to north-western Europe, i.e. the north and west of Spain and France, Belgium and the British Isles (Blackman & Rutter 1954; Roisin 1969; Fig. 1). It is characteristic of deciduous woodland on light, sandy-loamy soils and is generally absent from fully developed mor soils or heavy soils. It prefers a sandy to loamy soil texture and a well-balanced water regime (Roisin 1969), avoiding compacted soils or stagnating water. The pH-optimum varies between 5.5 and 6.5. The greater part of the seasonal growth is completed before the light intensity falls to a minimum (Blackman & Rutter 1954). A new root system is produced annually and becomes infected by mycorrhiza very quickly after the roots emerge from the bulb (Daft *et al.* 1980; Merryweather & Fitter 1995; Merryweather & Fitter 1996). Extension of the radical, linear leaves starts approximately in the middle of March followed by the extension of the inflorescence a month later, the flowers unfolding in early May (Blackman & Rutter 1954). The fruit consists of an ovoid capsule of approximately 1.5 cm, with several black, globular seeds

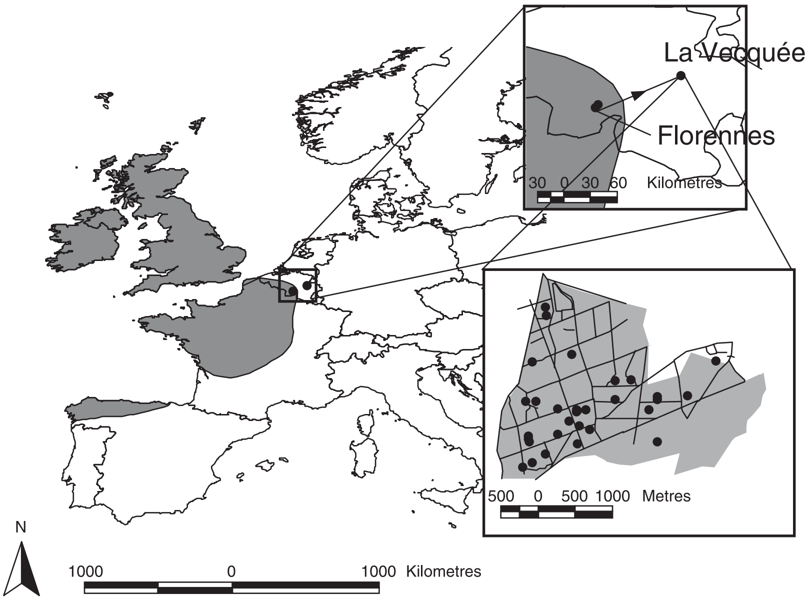

Fig. 1 Distribution of *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. in western Europe (compiled from Blackman & Rutter 1954; Knight 1964; Roisin 1969). Inset 1: location of the source populations (Florennes) and the implanted populations (La Vecquée). Inset 2: detail of the study area with implanted populations as black dots.

(*c*. 2 mm) in each cell. Dispersal by seeds is the main recruitment mechanism, although clonal reproduction (by daughter bulbs) also occurs frequently (Blackman & Rutter 1954; Knight 1964).

Salisbury (1942) reports an average seed weight of 5–6 mg, an average number of viable seeds per plant of 91 ± 4.0 and a production of ±500 seeds m^{-2} in a dense population in Great-Britain. The seeds fall from the capsule close to the plant in July. Knight (1964) reports an average recruitment distance of 40 cm and a maximum distance of 81 cm, based on seedling occurrence at the margin of a number of dense but isolated populations with clearly defined margins. The seeds germinate in autumn when temperatures drop below 11 °C (Thompson & Cox 1978). Before the next spring, almost all viable seeds germinate, so no persistent seed bank develops (Thompson *et al*. 1997). Plants flower for the first time around the fifth year (Woodhead 1904). In contrast to picking of the inflorescence (Peace & Gilmour 1949), mowing or grazing and trampling have been reported to have an adverse effect on both growth and on the storage of assimilates in the bulb (Blackman & Rutter 1954).

EXPERIMENTAL SET-UP IN 1960

Bulbs of *Hyacinthoides non-scripta* were transplanted from three source populations to 27 small groups of 7–10 individuals in the Vecquée forest in autumn 1960 (Table 1 and see Appendix S1 in the Supplementary Material). The source populations were situated in the Florennes forest, approximately 120 km to the west of the Vecquée forest inside the range of *Hyacinthoides non-scripta* (Fig. 1). The bulbs were planted at the same depth at which they were collected. Both source and introduced populations were numbered and marked on a topographic map (scale 1/10.000) for future resurveying, and soil type, canopy layer and description of the herb layer in the next spring using the Braun-Blanquet method, were all noted. Plot sizes for vegetation description were 10 × 10 m, with the newly introduced bulbs situated in the centre of the plot.

RESURVEY OF THE POPULATIONS IN 2005–06

At all locations (including the source populations), pooled samples of 20 soil cores, 1.5 cm in diameter and 15 cm deep, were collected and analysed for pH, phosphate, magnesium, calcium, potassium, sodium concentrations, and carbon content. Canopy layer and field layer were described, the latter using the same Braun-Blanquet method as Rogister in 1960. An ordinal five-class forest management variable was constructed and assigned to each of the locations (based on information from the National Forest Service and by best professional judgement) to account for changes in composition and structure of the tree layer between 1960 and 2005: (i) no changes; (ii) changes only in the shrub layer; (iii) changes in secondary tree species; (iv) changes in dominant tree species; and (v) clear-cut and eventually reforestation. In an analogous way, an ordinal soil disturbance variable was constructed, describing visual signs of disturbance (e.g. trampling by wild boar, logging trails) with five classes: (i) undisturbed; (ii) moderate disturbance in a small part of the plot; (iii) moderate disturbance in a large part of the plot; (iv) severe disturbance in a small part of the plot; and (v) severe disturbance in a large part of the plot.

All 27 locations where the bulbs had been introduced were labelled 'occupied' or 'unoccupied', based on different visits in spring 2005 and 2006. As the 11 populations that were relocated could be located with reasonable precision (±3 m) using the original maps and GPS, we assumed that all populations that could not be relocated had become extinct. For small populations, all individuals were mapped and digitized using GIS software (ESRI 2001). For large populations, the edges of all uniform patches were mapped, and the population density was estimated in randomly chosen 0.5×0.5 m^2 samples. Only isolated individuals were mapped individually, in an attempt not to damage the populations. Isolated individuals were searched by walking in a spiral manner around the populations up to a distance of 50 m. As the species is very distinctive (fresh, green leaves and purple inflorescences at a time when there is almost no other vegetation) the chance of missing isolated individuals was very low.

Population density (m^{-2}) and proportion of flowering individuals were measured in randomly selected 0.5×0.5 m^2 plots. Population size (i.e. the number of individuals) was calculated by multiplying the estimated population density and the calculated area of the same population (m^2). The mean migration distance of the population was calculated both as the mean distance from the population mass centre to the edge of the main, dense population in 18 directional sectors (i.e. every 20°) and as the mean distance from the population mass centre to the furthest individual, in the same 18 directional sectors (cf. Heinken 2004). It was thus assumed that population expansion started from the mass centre of the population.

The performance of the individuals in both source and introduced populations was investigated by measuring vegetative and reproductive plant traits: length of the longest leaf (cm), plant (inflorescence) height (cm), number of flowers per plant and mean seed weight (mg). The first three variables were measured at flowering time (early May) in 10 randomly chosen flowering plants per population (or the maximum number of flowering individuals if there were less than 10), the last at seed ripening (early July). At least 30 seeds per population were collected and weighed in the laboratory.

DATA ANALYSIS

The soil characteristics matrix was ordinated using principal component analysis (PCA) and ordination scores for both extinct and extant populations were tested for differences using Mann–Whitney test statistics. The vegetation matrix, containing both the vegetation descriptions from 1960 and 2005 for all 27 locations in the Vecquée forest and the three source populations in the Florennes forest, was ordinated using non-metric multidimensional scaling (NMS) (see Clarke 1993). Before running the NMS, the Braun-Blanquet classes were converted into a rank order scale as proposed by van der Maarel (1979), and species occurring in fewer than three samples were excluded. Distances between the 1960 and 2005 descriptions (for the same population) in the ordination diagram were measured by simple Euclidean distance and related to survival/extinction. Mann–Whitney *U*-tests (Siegel & Castellan 1988) were used to examine associations between the disturbance and forest management variables and survival/extinction of the implanted populations. Differences in performance between the source and implanted populations were analysed by independent-samples *t*-tests (with 95% confidence interval).

A two-parameter Weibull probability density function (*pdf*) was calculated for both the migration distances based on the population front and the furthest individuals. The *pdf* formula is given by:

$$f(x,\alpha,\beta) = \frac{\alpha}{\beta}\left(\frac{x}{\beta}\right)^{\alpha-1} \exp\left(-\left(\frac{x}{\beta}\right)^{\alpha}\right) \text{fox } x \geq 0,\ \alpha > 0,\ \beta > 0$$

where α is a shape parameter and β a scale parameter.

This function was used: (i) to describe and compare the migration distances based on the major population front and the furthest individuals; and (ii) to calculate the expected spread rates for the next 45 years. The Weibull *pdf* was fitted based on 162 distances for each data set (main population front and furthest individuals), divided into nine equal-distance categories. We used a standard bootstrap method (10 000 random samples, with replacements, of 162 distances) to estimate 95% confidence intervals for the fitted parameter values and the probability density function.

Results

Of 27 introduced populations in 1960, 11 (41%) still survived and were reproducing after 45 growing seasons, and 16 (59%) had become extinct. In the PCA of the soil characteristics, the first axis explained 45% of the variation, and the second axis 36% (Fig. 2). Variation in the soil samples was principally determined by differences in soil productivity (PCA axis 1) and pH (PCA

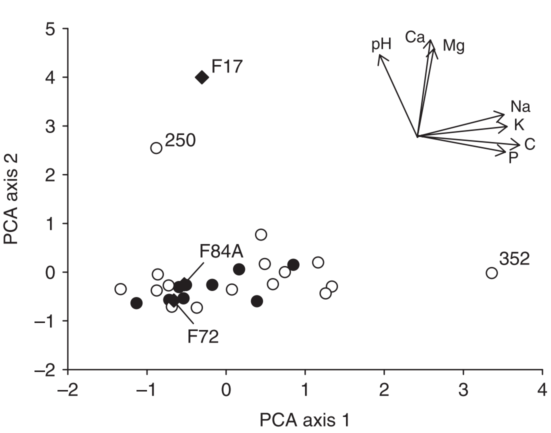

Fig. 2 PCA diagram containing the ordinated soil samples of all studied locations. Soil samples taken from locations with extant populations are shown as black circles, samples from locations with extinct populations as open circles and soil samples from the three source populations as black diamonds. Outliers and source populations are labelled.

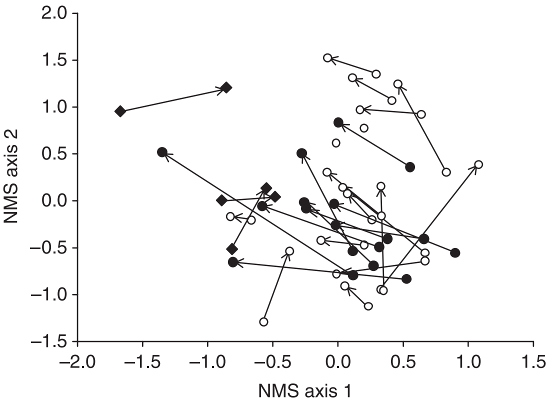

Fig. 3 NMS diagram containing the ordinated vegetation relevés of all studied locations, both in 1960 and in 2005. Relevés taken from locations with extant populations are shown as black circles, relevés from locations with extinct populations as open circles and relevés from the three source populations as black diamonds. Two locations had no 1960 relevés. The distances populations travelled in the NMS diagram from 1960 to 2005 are shown as arrows.

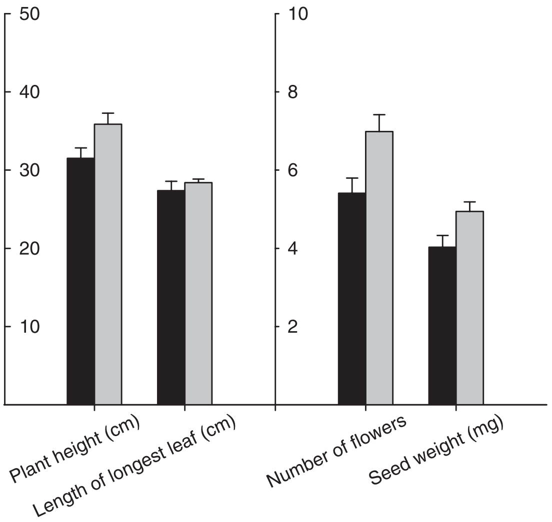

Fig. 4 Differences in overall performance characteristics between implanted populations (black) and source populations (light grey). Bars represent overall mean ± standard error.

axis 2). However, there was no clustering of locations with either extinct or extant populations in the soil characteristics PCA diagram, clearly suggesting that soil properties (within the range of soils occurring in the study area) were not an important factor in the survival of the experimentally introduced populations (Fig. 2).

Comparison of extinct and extant populations indicated forest management as a strong determinant of long-term population survival: stronger impact in the tree layer was associated with higher extinction probability (Mann–Whitney test, $Z = -2.587$, $P = 0.010$). An even stronger effect was found for physical disturbance of the forest soil (Mann–Whitney test, $Z = -3.029$, $P = 0.002$). Both disturbance variables were strongly correlated ($r_s = 0.707$, $P < 0.001$).

Herb layer composition in the source populations of *Hyacinthoides non-scripta* differed in position from the vegetation composition at the locations of implantation (Fig. 3), but there was no relationship between survival probability and the locations of the 1960 relevés in the NMS diagram (Table 2). Significant correlations were found for both location and shift on the second axis, and total distance travelled in the NMS diagram (Table 2).

The general performance of plants in the implanted populations was generally lower than that of plants in the populations from which they originated (Fig. 4); however, only the difference in number of flowers was significant (Mann–Whitney *U*-test; $Z = -2.031$, $P = 0.042$). Marginally significant trends were present for plant height ($Z = -1.690$, $P = 0.091$) and seed weight ($Z = -1.709$, $P = 0.087$). Comparison of the performance of the individuals of source and implanted populations showed significant differences for all four traits in three out of five populations where the exact origin was known (Table 3 and see Table S1 in Supplementary Material). These results generally hold for the other populations (including the largest population, 23) when compared with all three possible source populations (data not presented). Densities and proportions of non-flowering individuals in the introduced populations were generally equal to or higher than those in the source populations, especially in the largest introduced populations (Table 1).

The mean radius ranged from 0.25 m to 2.68 m or radial spread rates from 0.006 my^{-1}–0.06 my^{-1}.

The two-parameter Weibull probability density function fitted the migration distances based on the main population front and the furthest individuals ($R^2 = 98.1$ and 99.7, respectively; Kolmogorov-Smirnov tests). The former was characterized by a shape parameter $\alpha = 1.11$ (0.98–1.29 bootstrap 95% confidence intervals) and a scale parameter $\beta = 0.98$ (0.86–1.13), while the latter was characterized by $\alpha = 0.88$ (0.72–1.02) and $\beta = 1.47$ (1.26–1.77). The resulting effective dispersal kernels (dispersal kernels incorporating both dispersal and establishment) (Nathan *et al.* 2003) drop off rapidly with distance, especially for the distances of the main population front (Fig. 5). The principle statistics for the effective dispersal kernels of the main population front and the furthest individuals are, respectively: mean 5.86 and 13.93 m, median 0.71 and 0.97 m, and standard deviation 2.88 m and 7.60 m.

Discussion

The experimental introduction of bluebell bulbs resulted in reproducing populations in 41% of the sites after 45 years. Habitat quality in terms of soil chemistry or vegetation composition did not affect the probability of long-term survival of the experimental populations. While similar results were obtained for *Dentaria bulbifera*, another perennial forest herb of deciduous forests

Table 1 Statistics of the extant *Hyacinthoides non-scripta* populations and the source populations. Variables shown are population code (according to Rogister's code), the number of implanted bulbs in 1960, the current population size, proportion of flowering individuals, population density and area. For two heavily disturbed populations, 298 and 382, area and density are not relevant

Code	Number of implanted bulbs*	Number of individuals	Proportion flowering/total	Density (m^{-2})	Area (m^2)
305	10	38	0.71	165	0.23
184A	7	49	0.84	210	0.29
190	7	101	0.61	144	0.7
215	7	132	0.80	105	1.56
298	10	20	0.83	NA	NA
308a	7 or 10	2235	0.31	317	7.05
308b	7 or 10	436	0.36	248	1.76
308c	7 or 10	218	0.53	168	1.3
23	7 or 10	6453	0.33	246	26.23
382	7 or 10	6	1.00	NA	NA
390	7 or 10	1509	0.31	280	5.39
Source populations					
F17	NA	NA	0.53	188	NA
F72	NA	NA	0.46	196	NA
F84	NA	NA	0.74	76	NA

*When not exactly known (7 or 10), we assumed 10 for further analyses.

Table 2 Mann–Whitney comparisons between extinct and extant populations. Tested variables are the locations of the soil samples in the soil PCA diagram, the locations of the 1960 and the 2005 vegetation relevés in the vegetation NMS diagram and the distance travelled (shift) in the vegetation NMS diagram from 1960 to 2005, measured by Euclidean distance

	Soil		1960 vegetation		2005 vegetation	
	Z	*P*	*Z*	*P*	*Z*	*P*
PCA axis 1	–0.736	0.462				
PCA axis 2	–1.019	0.308				
NMS axis 1			–0.567	0.571	–2.661	0.008
NMS axis 2			–0.630	0.529	–0.623	0.533
Shift in axis 1					–3.276	0.001
Shift in axis 2					–1.323	0.186
Total shift					–2.268	0.023

Table 3 Summary statistics of performance characteristics and *t*-test comparisons between individuals of source and implanted populations. Notice that the origin of the bulbs was only exactly documented for five of the transplanted populations

	Source population				Implanted population				
Variable	Code	*n*	Mean	SD	Code	*n*	Mean	SD	Significance *P*
Plant height (cm)	17	25	38.36	5.41	305	5	30.40	3.80	0.004
	72	25	33.48	6.33	184A	5	23.20	4.32	0.002
		25	33.48	6.33	190	5	27.60	3.44	0.055
		25	33.48	6.33	215	10	32.60	5.60	0.704
	84	25	35.76	4.95	298	5	29.00	4.80	0.009
Length of longest leaf (cm)	17	25	28.08	4.23	305	5	23.20	3.03	0.021
	72	25	27.84	5.45	184A	5	23.20	3.19	0.079
		25	27.84	5.45	190	5	23.20	3.70	0.081
		25	27.84	5.45	215	10	27.20	3.19	0.670*
	84	25	29.28	4.40	298	5	27.80	3.70	0.489
Number of flowers	17	25	6.92	2.64	305	5	3.80	0.45	0.001*
	72	25	6.28	3.27	184A	5	6.20	1.64	0.958
		25	6.28	3.27	190	5	3.60	1.14	0.004*
		25	6.28	3.27	215	10	7.40	3.89	0.392
	84	25	7.76	4.51	298	5	6.60	2.30	0.583
Seed weight (mg)	72	30	4.63	0.98	190	7	3.47	0.89	0.007
		30	4.63	0.98	215	30	2.98	0.60	0.001*

**t*-test with equal variances not assumed; all others equal variances assumed.

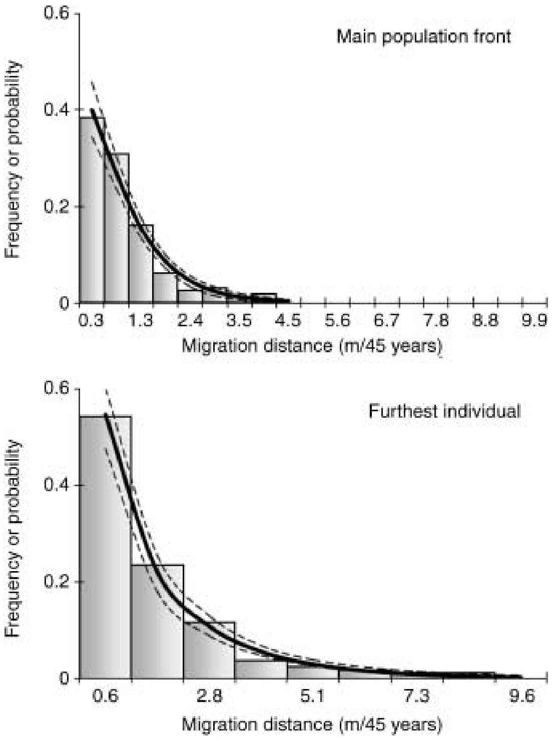

Fig. 5 Summary of observed (columns) frequencies of migration distances and the corresponding fitted (lines) probabilities of a two-parameter Weibull probability density function, based on the main population front (upper) and the furthest individuals (lower). The case of the main population front is characterized by a higher shape parameter (resp. $\alpha = 1.11$ vs. $\alpha = 0.88$) and thus thinner tail, and by a lower scale parameter (resp. $\beta = 0.98$ vs. $\beta = 1.47$) and thus lower migration distances in comparison with the case of the furthest individuals. The 95% confidence intervals (dashed lines) were calculated by 10 000 random bootstrap samples.

(Gustaffson *et al.* 2002), these results do not seem to hold for many grassland species (Klinkhamer & de Jong 1988; Barret & Silander 1992; Kiviniemi & Eriksson 1999). It has been suggested that this must be attributed to the less dense field layer vegetation cover in deciduous forests compared with grasslands (Gustaffson *et al.* 2002). However, although there is no clear cluster separation of extinct and extant populations in the soil characteristics PCA diagram, the subset of extant populations occupies a more restricted space than the whole set of introduced populations. This pattern is consistent with the notion that survival is possible only under a certain range of soil properties, but this by itself does not guarantee success. In contrast to the other local factors investigated, physical disturbance of the forest soil and forest management showed clear effects on long-term population survival. Leaves develop from initials laid down in the previous year, and if they are destroyed, no more are produced that year. Consequently, severe disturbances such as trampling by animals or humans, damage by tree-logging, mowing and grazing have very adverse effects on both growth and on the storage of assimilates in the bulb, an effect which is greater the earlier in the year the damage occurs (Peace & Gilmour 1949; Blackman & Rutter 1954).

The apparently lower performance of the individuals in transplanted populations compared with their source populations could indicate decreasing site suitability, as we would expect outside the range of the species. However, densities of individuals and proportion of non-flowering individuals were generally equal to or even higher in the introduced populations, especially in the largest populations, indicating that the carrying capacity, as a measure for habitat quality, does not seem to be inferior to that of the habitats supporting the source populations (Hoffmann & Blows 1994). These results suggest that the introduced populations are not at equilibrium yet, but in a phase of expansion containing more younger and thus smaller individuals. This is also in agreement with other performance variables: lower plant height, numbers of flowers and seed weight are probably due to younger population structure in the introduced populations, and not due to site unsuitability. This is also supported by the field observation of a decline in performance from the centre to the edge in the largest populations. Moreover, most growth rates are positive (ranging from 0.99 to 1.13 based on the number of flowering individuals). Nevertheless, realized migration rates were extremely low, with those estimated for the main population front varying from < 0.01 to only 0.06 m per year over a period of 45 years.

To assess the potential for future spread of these populations, we combined data on fecundity (Salisbury 1942), population size and density (Table 1), and the effective dispersal kernels fitted to observed migration distances. Focusing on the largest population (code 13 in Table 1), we applied a two-step procedure to estimate the highest potential for spread in the next 45 years. In the first step, we calculated the total fecundity (number of viable seeds produced in 45 years) of this population as 8.8 million seeds over 45 years (= 6543 individuals × 0.33 fraction of fertile individuals × 91 seeds individual^{-1} year^{-1} × 45 years). Multiplying this fecundity by the Weibull cumulative density function with the corresponding shape and scale parameters revealed that the front of this population is expected to be located 11.91 m from the current population front after another 45 years, while the furthest individual is expected to be located 34.31 m away. These calculations underestimate fecundity because they do not account for population growth during this period. Thus, in the second step we repeated the same calculations, but estimated fecundity of the expanding population from the population spread estimates in the first step, assuming symmetrical radial expansion of 11.91 m. The total fecundity calculated for this scenario is 229 million seeds in 45 years (= 246 individuals $\text{m}^{-2} \times 688\ \text{m}^2$ $\{= \pi[(26.23/\pi)^{1/2} + 11.91]^2\}$ × 0.33 fraction of fertile individuals × 91 seeds individual^{-1} year^{-1} × 45 years). Under this rather extreme scenario, the expected migration distances of the main population front and the furthest individual remain very limited, only 14.07 and 42.35 m, respectively, after 45 more years.

Other authors have estimated migration rates of *Hyacinthoides non-scripta* in populations situated more or less in the centre of its range. Rackham (1980) mentions colonization rates of *c.* 100 m per century. Pigott (1982), however, records figures of 6–10 m per century. Honnay *et al.* (1999) report an average colonization distance of 32 m and a maximum of 55 m per century. The migration distances observed here, and also those estimated for the next 45 years, are thus situated on the lower end of the published range of estimates. Our results might be conservative, as colonization of the experimental populations was assumed to start from the mass centre of the current populations. However, as in the current study, 7–10 bulbs were planted and possible long-distance dispersal will probably consist of one to a few seeds. The initial phase of population establishment will be prolonged in natural colonization and will only occur if the dispersed seed(s) establish successfully.

Colonization rates based on the furthest individual were typically twice as high as those based on the main population front. The shape of the calculated Weibull probability density functions shows a thinner tail for the migration distances based on the major population front (due to a higher shape parameter, resp. $\alpha = 1.11$ vs. $\alpha = 0.88$), and shorter (mean = 5.8 vs. 13.93 m) and less variable (s.d. = 2.88 vs. 7.60 m) migration distances in comparison with the case of the furthest individuals (Fig. 5). As illustrated in our analysis of the expected rates of spread in the next 45 years, the colonization process is expected to be driven by establishment of isolated individuals, eventually developing to small satellite populations, which are later absorbed by the advancing front of the main population.

We can conclude that the regional distribution of *Hyacinthoides non-scripta* is dispersal limited. Population survival appears to be independent of soil type (within the range of soils occurring in the study area) and changes in the composition of the herb layer. In contrast, physical disturbance of the soil and major changes in the tree layer by forest management are the main determinants of population extinction. Plant performance was generally lower in the introduced populations than in the source populations, but densities and proportion of non-flowering plants were equal to or higher, especially in the largest populations. This suggests that these populations are still in an expansion phase with more, but younger and thus smaller, individuals. These long-term experimental data may be representative of population spread for slow dispersing (mainly ballistic, barochore or myrmecochore) forest plant species after occasional long-distance dispersal events, e.g. by human introduction. However, the slow rates of spread indicate that, even if such events occur, it can take a very long time to establish viable population sizes. Nevertheless, long-term data on establishing and spreading plant populations remain very scarce. We therefore encourage other ecologists to record transplant experiments as long as possible for other forest species.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Characteristics of the source and transplanted populations of *Hyacinthoides non-scripta*.

Table S1 Performance comparison for populations where the exact origin was not known.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2006.01208.x