Metapopulation viability of an endangered holoparasitic plant in a dynamic landscape

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By creating transient patch mosaics, disturbance can influence the dynamics of interacting populations in many ecosystems. In European heathland, traditional land use created such dynamic systems favourable for both early and later successional species. Little empirical evidence is, however, available on the impact of current management on metapopulations occurring in such landscapes. This paper looks at the metapopulation viability of the endangered holoparasite Cuscuta epithymum, a species that typically occurs in early successional stages of recently managed heathlands. We used both observational and experimental data from a 4-yr study to parameterise a spatially explicit metapopulation model. This model explores the impact of demographic characteristics and spatiotemporal landscape patterns created by management events on metapopulation viability. Both occasional long-distance dispersal and dormant seeds are shown to be critical for the long-term survival of C. epithymum in a dynamic heathland landscape subjected to a fixed rotational mowing of 15 yr. A relatively high management frequency (<15 yr between two consecutive mowing events) appeared to be necessary to sustain a viable C. epithymum metapopulation. When there is a longer interval between management events, grazing can counterbalance the negative effects of vegetation succession. Our results indicate that small-scale cyclical management events combined with extensive grazing are the most appropriate management strategy to maintain viable populations of C. epithymum instead of the current large-scale management events. Our results further emphasise the importance of incorporating both spatiotemporal patch availability and key demographic characteristics, especially seed banks, for a realistic view of metapopulation dynamics in disturbed landscapes. This study clearly demonstrates the usefulness of metapopulation models to understand the impact of management events and to provide new ecological insights into processes acting at a landscape scale.

Disturbance is an important component of many ecological systems, influencing both populations and metapopulations by creating a spatiotemporal mosaic of patches at different successional stages (Moloney and Levin 1996). The impact of disturbance on the distribution and dynamics of a species within a specific landscape is expected to depend on both the spatiotemporal disturbance patterns and on the species’ demographic characteristics (Moloney and Levin 1996, Matlack and Leu 2007). The long-term impact of disturbance on metapopulations of rare species may be crucial for management strategies, but only a limited number of studies have incorporated the auto-ecological characteristics of the focal species with the dynamics of the landscape. This is especially true for plant metapopulations where the majority of the published literature involves theoretical work (Husband and Barrett 1996, Higgens and Cain 2002). Although a few authors have demonstrated the impact of seed emigration and plant life-span on metapopulation viability in disturbed landscapes (Johst et al. 2002, Verheyen et al. 2004, Bossuyt and Honnay 2006, Matlack and Leu 2007), empirical evidence about the effect of seed banks on metapopulation viability is missing. This may be particularly important for early successional species occurring in dynamic landscapes, where establishment of a seed bank may function as an important strategy to buffer populations against local extinctions during unfavourable conditions (Bossuyt and Hermy 2003, Fenner and Thompson 2005, Piessens and Hermy 2006).

Heathlands in Europe emerged as an anthropogenic landscape ca 7000 to 4000 yr ago as the result of forest clearance followed by millennia of small-scale management activities, such as grazing, turf cutting, burning and mowing (Webb 1998, De Blust 2004, Piessens et al. 2004). As a result, semi-natural heathland systems often provide a habitat for many species relying on particular successional stages, which are the result of heathland management
Diphasiastrum tristachyum is a typical heathland species, such as Gentiana pneumonanthe, even-aged vegetation (De Blust 2004). During last decades, conservation management is often applied at a large-scale, thus succession towards woodland and thus avoid further loss of conservation strategies are applied now to stop natural degradation and loss of heathland habitat (Webb 1998, Piessens and Hermy 2006). In many heathland areas, however, traditional land-use practices have declined because their populations may quickly collapse in the absence of continued disturbance. Long-term survival of these early successional species can only be assured when the loss of local populations is counterbalanced by the establishment of new populations through (re)colonisation of newly created patches. Despite the well-known effects of different disturbance regimes on community organisation and diversity (Bullock and Pakeman 1997, Vandvik et al. 2005), underlying mechanisms of plant population dynamics have received little attention. Consequently, there is a need to examine the impact of temporal and spatial variation in habitat suitability on individual species performance, (meta)population dynamics and long-term survival.

In this study we focus on the effects of demographic traits and spatiotemporal landscape patterns created by management events on metapopulation dynamics and long-term survival of the early successional holoparasite Cuscuta epithymum. This endangered species grows on un lignified young heather and typically appears after heathland vegetation has been set back to an earlier successional state (Meulebrouck et al. 2007, 2009). Like many other species living in similar semi-natural landscapes, Cuscuta epithymum is generally restricted to young patches of heathland vegetation (mostly Calluna vulgaris), typically with a loss of host-plant quality through natural succession to old, unsuitable heather (Meulebrouck et al. 2007). The combination of directional vegetation change through time, and occasional vegetation disturbance events results in Cuscuta epithymum showing spatiotemporal dynamics with colonisation in newly created patches of young heather and extinction from patches containing heather growth >7 yr. The heathland system under study is a rare example of a system in which both the ecology of the focal species and the dynamics of the landscape are well documented (Meulebrouck et al. 2007, 2008, 2009). It provides an excellent opportunity to investigate the interacting effects of demographic characteristics and management-induced spatiotemporal landscape dynamics on metapopulation viability. In particular, the following questions were addressed: 1) what are the relative contributions of seed emigration, seed bank persistence and adult life-span to metapopulation survival in a dynamic landscape? 2) What type, frequency and spatial arrangement (including patch size and isolation) of management events are needed to provide a reasonable chance of Cuscuta epithymum surviving the next 100 yr? To answer these questions we used a stage-structured, spatially explicit metapopulation model whose parameters are founded on an extensive data-set originating from 4 yr of field observations combined with experimental data collected in four heathland systems.

### Materials and methods

#### Study species

Cuscuta epithymum (var. (subsp.) epithymum; Convolvulaceae) is a rootless and leafless holoparasite dependent on other plants for nutrition (Kuijt 1969). In Flanders, as elsewhere in north-western Europe, this species is mainly found in dry, recently managed Calluna-dominated heathland (Doyle 1993, Meulebrouck et al. 2007). Cuscuta epithymum is rapidly declining in several western European countries (Weeda et al. 1988, Cheffings and Farrel 2005) and is categorised as “endangered” on the recent Red List of Flemish phanerogamic plants (Van Landuyt et al. 2006).

During its life span, Cuscuta epithymum has three important stages: seeds, adults originating from germinated seeds (adult from seed) and adults originating from overwintering haustoria (adult from haustorium; Fig. 1). The transition from one stage to another occurs over a 1-yr interval (Fig. 1). Seeds produced in any one autumn will remain close to the parent plant or disperse to other patches, and they will germinate in the next spring, enter in a persistent seed bank or die. Seedlings observed during spring are assumed to be both the result of germination of seeds in the persistent seed bank or from those dispersed (seed rain) the previous autumn (unpubl.). To establish an adult originating from seeds, seedlings only have a maximum of 21 d to locate a suitable host or they die. The host is mainly a young Calluna vulgaris individual in dry heathland vegetation and is infected by Cuscuta epithymum through haustorial connections through which nutrients are taken from the host’s vascular tissue (unpubl.; see also Meulebrouck et al. 2007, 2008). Adults can also originate from haustoria that overwinter vegetatively in the host’s tissue, sprouting again in the following spring (i.e. adult from haustorium; Meulebrouck et al. 2009). When seedling establishment or haustorial sprouting is successful, adult plants of Cuscuta epithymum form aggregations of red thread-like stems, with white autogamous flowers during summer (Verdcourt 1948, unpubl.). At the end of the autumn, after seeds are shed, only dried, dead segments of Cuscuta epithymum stems remain visible. Cuscuta epithymum re-establishes each spring from overwintering haustoria and/or germination from the seed stage as long as young C. vulgaris individuals are present (Meulebrouck et al. 2007). When a disturbance event converts a late-successional heathland patch into a young-successional patch, Cuscuta epithymum may colonise by germination of recently-dispersed seeds or by recruitment via the seed bank.

#### Field populations and plant trait measurements

During 2004–2008, we investigated 108 Cuscuta epithymum populations in 289 patches in four nature reserves, located in north-eastern Flanders (Belgium; Meulebrouck et al. 2007). Distance between these four nature reserves ranges
between 2.4 and 12.4 km (Meulebrouck et al. 2007). The reserves are seen as isolated heathland fragments among which no interaction occurs. The nature reserves contain dry heathland vegetation, typically dominated by heather (C. vulgaris). A rotational management strategy of mowing, sometimes in combination with extensive grazing (cattle or horses), is applied to restore and conserve the heathland vegetation. This rotational strategy creates a dynamic landscape of patches of variable time since last disturbance and has a range of successional stages. Within such heath vegetation, C. epithymum typically shows a patchy spatio-temporal distribution. Canopy closure during heathland succession causes population decline and extinction of the above-ground population, although the seed bank may persist. In such dynamic landscapes, metapopulations can be seen as a permanently changing system of suitable patches in which colonisation and extinction change with the local heathland dynamics. Each summer, we investigated all appropriate C. epithymum habitat patches (i.e. recently mown patches typically containing young C. vulgaris individuals, Meulebrouck et al. 2007), allowing us to understand patch dynamics, including changes in host quality (patch suitability), establishment and disappearance of appropriate habitat patches, and population dynamics of C. epithymum populations. In each of the surveyed patches, measurements were made of patch size, patch isolation, characteristics of the vegetation (vegetation height and cover), and the size and fecundity of each C. epithymum population (see Meulebrouck et al. 2007 for further details). Seed germination and seed sowing experiments were carried out to evaluate germination and establishment rates under both controlled laboratory and field conditions (Meulebrouck et al. 2008 and unpubl., respectively). In the last mentioned experiment the effect of heathland management events, degree of vegetation succession and seed-density on C. epithymum establishment was examined during two consecutive growing seasons. A seed bag burial experiment, in which fresh C. epithymum seeds were buried in the field under natural conditions for up to 31 months, was established to quantify seed mortality rates in soil (unpubl.). Finally, we quantified the amount of over-wintering as haustoria in a subsample of the studied populations (Meulebrouck et al. 2009).

**Modelling**

We modelled the dynamics of C. epithymum metapopulations with a spatially explicit, stage-structured stochastic simulation model implemented in RAMAS/Metapop.
Akçakaya 2002 for further details). This model uses x- and y-coordinates to define the spatial metapopulation structure and captures annual intra-patch population dynamics (Johst et al. 2002). Density dependence based on a ceiling function without the Allee effect is included in the model, which affects vital rates. Environmental stochasticity was included in the model by means of temporal variation in vital rates, which are identical for each patch, but change each time step. Temporal variation in vital rates was achieved by using the coefficient of variation for fecundity (CVF = 1.51) and for survival (CVa = 0.82), derived from observed variation in the study area over a 4-yr period. Demographic stochasticity was included in the model by using the demographic stochasticity feature in RAMAS (Akçakaya 2002). Since such between-years dynamics cannot be captured by single season survey data, between-year stochasticity was achieved by using data from four consecutive years (Peltzer et al. 2008). Each simulation was run for 100 yr, with 1000 replications.

Experimental landscape structure and demographic variables

The hypothetical “landscape” used in the model is based on the sizes, spatial arrangement and successional stage of the 289 patches observed during four years of research. It is constructed as a square lattice of 100 cells (further referred as “patches”). Each of these 100 patches represents a 400 m² piece of heathland vegetation, together comprising a 4 ha mosaic landscape of adjacent patches with variation in time since the last management event (Fig. 2). The used patch size is based on the average (.±SE) patch area of 393 ± 48 m² found for management patches in the reserve Heiderbos. A “landscape” of 4 ha simulates the size of many heathland fragments in Belgium and other countries in western Europe (Decleer and De Belder 1999, Rose et al. 2000). Suitable patches for C. epithymum generally arise following management activities (such as mowing), after which host quality and patch suitability for C. epithymum gradually declines in time as the heather grows and gets older (i.e. vegetation succession). This changing patch suitability and associated deterministic extinctions was modelled by time-dependent carrying capacity (K) of a patch. The latter represents the maximum number of C. epithymum adults supported in a patch belonging to a particular succession stage, regardless of the number of seeds present in the seed bank. Following a patch management event, which resets the late-successional patch to a suitable patch containing young C. vulgaris, K is higher than 0 for a period of 10 yr, with a period of possible population growth immediately after intervention followed by a decrease of population size with vegetation ageing (Fig. 3). Depending on the frequency of the management intervention, each year a proportion of unsuitable habitat, i.e. late-successional vegetation in the hypothetical 4 ha landscape, is converted into suitable heath (newly mown vegetation) and gradually changes towards older heath vegetation. This gradual change of each virtual patch is based on the vegetation succession observed in the study area (Meulebrouck et al. 2007). At time step 0, each patch belongs to one of four conditions, which are suitable or unsuitable for presence of a persistent seed bank and/or aboveground populations is represented by dotted squares. The spatial distribution of C. epithymum populations, suitable and unsuitable patches and initial age of each patch (i.e. successional state; not presented) at the beginning of each simulation are based on real distribution patterns of C. epithymum populations and patches of different ages observed during 4-yr of research in four heathland reserves. The landscape modelled here is used as a starting point when simulating the variable demographic characteristics. At the beginning of each simulation each of the 100 patches was attributed to one of four different conditions: 1) unsuitable patch without seed bank (n = 20); 2) unsuitable patch with seed bank (n = 40); 3) suitable patch without seed bank (n = 14); 4) suitable patch with seed bank (n = 26).

C. epithymum growth, in combination with or without a persistent seed bank (Fig. 2). Only suitable patches may contain aboveground populations and consequently posses
a K higher than 0 at the start of each simulation. A persistent seed bank, on the other hand, can occur in both suitable and currently unsuitable patches.

For each virtual patch, the initial number of plants per population stage (seed, adult from seed and adult from haustorium) was calculated based on counts performed during 2004–2008 (Table 1). We used stage matrices to model the individual patch population dynamics. The lifecycle diagram for *C. epithymum* was translated into a transition matrix where the matrix elements $a_{ij}$ and $F_{ij}$ define transition probabilities from stage $j$ to stage $i$ in 1-yr time intervals (Caswell 2001, Fig. 1). The “fate” or “survival” transitions ($a_{ij}$) vary between 0 and 1, whereas “fecundity” transitions ($F_{ij}$) can have higher values. Transition probabilities in Table 1 were calculated from field data. For each simulation all 100 populations were attributed to the same transition matrix (Fig. 1).

In addition to the above mentioned general baseline of the model, we further applied two distinct steps in the analysis in order to evaluate the impact of three demographic characteristics of the species and to investigate the impact of management interventions in the long-run. We first investigated the possible influence of the three key demographic characteristics mentioned above on metapopulation viability by applying a fixed rotational management of 15 yr in each patch as shown in Fig. 3. We then modelled the impact of management events on *C. epithymum* metapopulations in the long-term with a fixed and realistic combination of demographic characteristics.

### Simulations of variable demographic characteristics under a fixed rotational disturbance regime

To explore the importance of a persistent seed bank ($a_{11}$ in the transition matrix), life-span ($a_{32} + a_{33}$) and seed emigration on metapopulation viability we ran 36 simulations, each with its own specific transition matrix (Fig. 1; Table 2). Three different levels of seed bank survival, i.e. percentage of seeds that is able to survive until the next growing season, were used in the simulations: low (7%), moderate (18%) or high (50%) seed survival (Table 2). Our seed burial experiment showed that the annual seed bank survival is on average 18% (unpubl.), and the other two values are chosen to be more extreme scenarios.

Research on overwintering haustoria has recently discovered the perennial character of *C. epithymum* (Meulebrouck et al. 2009), but the exact proportion of overwintering individuals and the impact on metapopulation dynamics is still not clear. We therefore incorporated variable life-span values of 0, 0.04, 0.10 and 0.25, representing an annual, very short, short or moderately perennial life-span, respectively (Table 2). Finally, to evaluate the effect of variable levels of seed emigration on metapopulation dynamics, simulations were performed in which variable levels of dispersal, i.e. variable fractions of all produced seeds leaving a particular patch, were used in the model. We used three fixed values of seed emigration: 4 seeds leaving the patch for every 10 000 seeds produced there, 1 and 3 seeds leaving the patch for every 1000 seeds produced (4/10 000, 1/1000 and 3/1000, respectively). The dispersing seeds were spread over all other patches in a distance-dependent way, following the dispersal function $\text{"Mij"} = a \exp \left(-\frac{D_{ij}}{b}\right)$ available in RAMAS/Metapop (with $M_{ij}$ the number of seeds in source patch $j$ that move to patch $i$, $b$ the rate of decline of the number of dispersers with increasing distance, $D_{ij}$ the distance between two patches and seed emigration rate $a$, Akçakaya 2002). Parameter $b$ is set high enough, at 200, to ensure that all patches have a reasonable chance of receiving dispersing seeds, with each successive patch receiving around

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value [mean ± SE]</th>
<th>Calculation method</th>
<th>Location</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size/patch&lt;sup&gt;1&lt;/sup&gt;</td>
<td>(1) 224 ± 49 (n = 288)</td>
<td>Mean population size for each vegetation age, including the total number of individuals belonging to stages “adult from seed” and “adult from haustorium”.</td>
<td>All</td>
<td>S 2004–2007</td>
</tr>
<tr>
<td>Seed abundance/patch</td>
<td>(2) 21.95 ± 1.55 (n = 570)</td>
<td>Based on population size and mean no. of flowers/individual&lt;sup&gt;2&lt;/sup&gt; × mean no. of seeds/flower&lt;sup&gt;3&lt;/sup&gt; + taking into account the linear relation between no. of seeds (Y) and vegetation age (X) (Y = −9.50X + 85.58; r^2 = 0.71; n = 81); seed mortality (30%) and germination rate (14%) the year after seed release.</td>
<td>All</td>
<td>S 2006–2007</td>
</tr>
<tr>
<td>$F_{22}$ and $F_{23}$</td>
<td>2.54</td>
<td>No. of reproduced seeds germinating in the following spring per adult; calculated from fecundity data; including seedling survival.</td>
<td>All</td>
<td>S 2006–2007</td>
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<td>$F_{12}$ and $F_{13}$</td>
<td>16.30</td>
<td>No. of reproduced seeds arriving in the seed bank per adult considering $F_{32}$, the 43% non-viable-died seeds and fecundity data; including seedling survival.</td>
<td>All</td>
<td>S 2006–2007</td>
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<tr>
<td>$a_{21}$</td>
<td>2.38%</td>
<td>Annual germination probability from seed bank discovered from seed burial experiment; including seedling survival.</td>
<td>MH</td>
<td>2006–2008</td>
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<tr>
<td>$\bullet$</td>
<td>14%</td>
<td>Seedling survival estimated from sowing experiment.</td>
<td>MH</td>
<td>Sp 2007</td>
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Table 2. Simulated (a) three demographic (dem.) characteristics with their parameter values and (b) various management scenarios used in the different scenarios of the basic model. Codes in parentheses refer to Fig. 1.

(a) Dem. characteristics     Modelling method     Parameter value range

Seed emigration     Fraction of produced seeds leaving the patch.     4/10 000 = low  
                    1/1000 = moderate  
                    3/1000 = high

Life-span \((a_{32} + a_{22})\)     Probability of adult to overwinter via haustoria.     0 = annual  
                    0.04 = very short-lived perennial  
                    0.10 = short-lived perennial  
                    0.25 = moderate-lived perennial

Seed bank persistent \((a_{11})\)     % of seeds in the seed bank remaining in the next year. Depends  
                    on germination from seed bank and seed survival rate.     7% = low  
                    18% = moderate  
                    50% = high

(b) Management actions     Interpretation     Scenarios

Patch distribution     Spatial location of the patches managed in the same year.     Clustered = patches in a block  
                    Random = random pattern

Grazing     Carrying capacity always \(\geq 30\) individuals.     1 = grazers present in landscape  
                    0 = no grazers present

Mowing frequency     No. of years between two consecutive mowing measures, modelled  
                    by changes in carrying capacity (no. patches mown yr\(^{-1}\)).     20 yr (5)  
                    2 yr (50)

50% fewer seeds than the next nearer patch. Low seed emigrations were used because it seems that the majority of \(C.\) \(e\)pithymum seeds disperse over very short distances and no clear dispersal event was observed during our field study. Upon arrival in a particular patch, dispersed seeds become part of the seed bank at the site irrespective of successional stage of the patch.

At the start of each of the 36 simulations, the landscape was exactly structured following the pattern shown in Fig. 2. The initial distribution of seed bank and the \(C.\) \(e\)pithymum populations (the four different conditions shown in Fig. 2) and change in successional state in each patch (i.e. time after the management intervention is applied to the vegetation, determined by K-value) are based on field observations during a 4-yr study. In each year six or seven of the 100 virtual patches were set back to initial successional state by mowing which represents a typical heathland management practice in the four studied reserves. This is equivalent to a rotational mowing or mowing frequency of 15 yr and is represented in the model by time-dependent carrying capacity \((K,\) as mentioned above, Fig. 3). The application of a rotational management of 15 yr on all patches prescribes the spatial structure of the landscape over the long-term. Finally, for each of the 36 simulations, a different combination of transition elements was used in the transition matrix, to test different combinations of demographic characteristics (Table 2).

Management scenarios

To examine the effects of different management regimes, particularly variable mowing frequencies, spatial arrangement of management events, and extensive grazing on \(C.\) \(e\)pithymum metapopulation viability, a virtual management experiment was performed. Using five different time-dependent K-series (as earlier mentioned for rotational mowing of 15 yr; Fig. 3), five mowing frequencies were created so that each patch was mown at 20, 15, 10, 4 or 2 yr intervals (Table 2). Mowing frequency refers to the frequency at which a particular patch is mown, expressed as the number of years between two consecutive mowing events. The higher the mowing frequency is, the shorter the period between two consecutive mowing events. With the five different mowing frequencies, the number of patches mown each year also fluctuated over time. Consequently, each time interval 5, 6–7, 10, 25 or 50 of the 100 patches were mown, respectively. When mowing frequency changes (by changing the K-value), the landscape structure represented in Fig. 2, also inevitable changes. For each of these five mowing frequencies, the model was run with a clustered or random spatial arrangement of managed patches. In the clustered arrangement mowing in a particular year was applied to adjacent patches, by which then a larger area of heathland patches with the same successional stage is formed. In the random arrangement patches were randomly mown across the 4 ha landscape matrix which tended to create small, isolated patches. In both types of spatial organisation, the number of annually mown patches and so the arrangement of the landscape depends on the mowing frequency. The model was also run with and without extensive grazing to examine the additional impact of grazing on metapopulation viability. Grazing creates young heather shoots and extends patch suitability, so K was always held higher than 30 individuals in the grazed situation. This number was based on long-term data of populations growing in the heathland nature reserve “De Maten” (50°5’7’N, 5°27’E), where grazing is used as an additional management tool. For all management scenarios, populations had a transition matrix with the same transition elements, including moderate seed
ability and time to extinction (Table 3 and 4a). When seed interaction with seed emigration reduced extinction probability, a lesser, but still significant amount, life-span and its increased metapopulation size after 100 yr (Table 3). To levels of seed emigration (1/1000 or 3/1000) significantlyween high seed persistence (50%) and moderate or high persistence and, more importantly with increasing seed decreased significantly with an increasing seed bank 400 m² with a fixed mowing frequency of 15 yr were

Both the extinction probability and the time to extinction of C. epithymum metapopulations occurring in patches of 400 m² with a fixed mowing frequency of 15 yr were decreased significantly with an increasing seed bank persistence and, more importantly with increasing seed emigration (Table 3 and 4a; Fig. 4). The interaction between high seed persistence (50%) and moderate or high levels of seed emigration (1/1000 or 3/1000) significantly increased metapopulation size after 100 yr (Table 3). To a lesser, but still significant amount, life-span and its interaction with seed emigration reduced extinction probability and time to extinction (Table 3 and 4a). When seed emigration increased to three seeds per 1000 leaving a patch, a remarkable increase of metapopulation size and decrease in extinction risk was observed (Table 3; Fig. 4).

Results

Demographic characteristics

Both the extinction probability and the time to extinction of C. epithymum metapopulations occurring in patches of 400 m² with a fixed mowing frequency of 15 yr were decreased significantly with an increasing seed bank persistence and, more importantly with increasing seed emigration (Table 3 and 4a; Fig. 4). The interaction between high seed persistence (50%) and moderate or high levels of seed emigration (1/1000 or 3/1000) significantly increased metapopulation size after 100 yr (Table 3). To a lesser, but still significant amount, life-span and its interaction with seed emigration reduced extinction probability and time to extinction (Table 3 and 4a). When seed emigration increased to three seeds per 1000 leaving a patch, a remarkable increase of metapopulation size and decrease in extinction risk was observed (Table 3; Fig. 4).

Management scenarios

The virtual management experiment showed that mowing frequency had the greatest affect on the survival probabilities of C. epithymum metapopulations (Table 4b; Fig. 5). Up to a certain point, increasing mowing frequency of a patch (i.e. the shorter the time between two consecutive mowing events), increases the chance that the metapopulation will survive for a period of 100 yr, with the species characterised by a fixed short life-span with a moderate seed persistence and a very low seed emigration rate (Table 4b; Fig. 5). With these demographic characteristics, C. epithymum metapopulation is guaranteed to persist over a 100-yr time interval, if a mowing frequency of 10 yr is applied in which 10% of the landscape is mown annually (Fig. 5). Once mowing frequency, however, exceeded 25 patches per year (i.e. 4 yr between two consecutive mowing events), the metapopulation size and its long-term survival probability decreased considerably (Fig. 5). The interaction of grazing with mowing frequency also explained a significant part of the observed variation in metapopulation abundance and the time to 50% extinction (Table 4b). In all management scenarios with the three lowest mowing frequencies (20, 15 or 10 yr between two mowing events), metapopulation size was significantly higher in extensively grazed landscapes than in ungrazed situations (Fig. 5). For the two lowest mowing frequencies (i.e. mowing frequency of 20 or 15 yr), a compensatory effect of grazing was observed, resulting in viable metapopulations after 100 yr where without grazing metapopulation extinction occurred (Fig. 5). When the frequency at which mowing events are applied increased, <10 yr between two consecutive mowing events, the effect of grazing was negligible (Fig. 5). The spatial arrangement of mowing applications, either random or clustered, had no significant impact on C. epithymum metapopulation persistence (Table 4b). Metapopulation viability was relatively similar under a clustered or random distribution of the management events, both with and without extensive grazing (Fig. 5).

Discussion

This study modelled the effects of varying demographic characteristics and different management scenarios on the response of a metapopulation of a short-lived early-successional species at the landscape level, and it provides clear insights on how both life-history traits and the spatiotemporal patterns of habitat patches in the landscape affect metapopulation viability in C. epithymum.

Importance of demographic characteristics

Early-successional species occurring in dynamic landscapes must be able to colonise new habitats at least as fast as they are lost from existing habitats in order to survive in the
long-term. Seed dispersal and the capacity to produce a persistent seed bank are generally viewed as adaptations to deal with this environmental stochasticity, permitting species to escape unsuitable conditions both in time and space and (re)colonise recently disturbed sites (Valverde and Silvertown 1997, Amarasekare and Possingham 2001). Although most metapopulation studies only consider seed dispersal in their simulations, the present study demonstrates that both seed dispersal and persistent seed banks may strongly decrease the probability of metapopulation extinction. The combination of a persistent seed bank with occasional long-distance dispersal can be seen as an optimal strategy to cope with the unpredictable availability of suitable habitat patches at the landscape scale. Whilst occasional long-distance seed dispersal increases the chance of colonisation of patches which become available, seed persistence ensures recolonisation of previously occupied patches after a period of unsuitability. Both life-traits additionally offer *C. epithymum* the opportunity to overcome unfavourable periods until the next management event. The interaction of both demographic characteristics may thus have a positive effect on metapopulation viability at the landscape scale (Table 4a), and highlights the need to incorporate seed persistence as an important demographic aspect in plant metapopulations.

Although *C. epithymum* seeds are generally categorised as “unspecialised for long-distance seed dispersal” (Kuijt 1969) and have no obvious adaptations for dispersal, seed resistance to sheep digestion is reported by several authors (Gaertner 1950, Kuijt 1969). Furthermore, Kuijt (1969) and Costea and Tardif (2006) reported evidence that *C. epithymum* seeds may occasionally disperse long-distances via epizoochory and even by means of management instruments (anthropochory). Since most European heathlands have traditionally been managed by large herbivores and mowing for many centuries, it might thus be plausible that livestock or transport in heather cutting, or movement as seeds stuck to tools/machines have played an important role in the dispersal of several early successional species, such as *C. epithymum* (Webb 1998, Lennartsson and Oostermeijer 2001, Couvreur et al. 2005). Our observations stress the importance of occasional long-distance dispersal for establishment of new populations in such highly dynamic landscapes, implying that more attention should be paid to potential long-distance dispersal agents, such as livestock and wild animals or even management machinery (Stryksra et al. 1997, Fenner and Thompson 2005, Peltzer et al. 2008). Finally, in contrast to the findings of Bossuyt and Honnay (2006), who investigated plant species in successional dune slacks, our results do not support a strong and positive effect of plant life-span on reducing the risk of metapopulation extinction. This can be attributed to the

| Table 4. F-values, $R^2$-adjusted and significance levels of the GLM-analyses testing (a) the relative influence of seed emigration, seed persistence, and life-span and their interactions on the time to metapopulation extinction and the metapopulation extinction probability after 100 yr and (b) the effect of mowing frequency, spatial management arrangement, grazing and their interactions on time to 50% extinction and metapopulation size after 100 yr. The model with the best F-ratio and highest $R^2$-adjusted was retained. |
| --- | --- | --- |
| **(a)** Variables | Time to extinction | Extinction probability |
|  | DF (n,d) | F | DF (n,d) | F |
| Seed emigration | 2,18 | 505.63*** | 2,18 | 289.06*** |
| Seed persistence | 2,18 | 192.37*** | 2,18 | 190.06*** |
| Life-span | 3,18 | 8.81** | 3,18 | 4.37* |
| Emigr. x seed pers. | 4,18 | 61.13*** | 4,18 | 70.74*** |
| Emigr. x life-span | 6,18 | 4.43** | 6,18 | 3.02* |
| R$^2$adj | 0.98 | 0.97 | 0.97 |
| **(b)** Variables | Time to 50% extinction | Metapopulation size |
|  | DF (n,d) | F | DF (n,d) | F |
| Frequency | 4,9 | 65792.26*** | 4,9 | 49008.56*** |
| Arrangement | 1,9 | 4.64ns | 1,9 | 2.55ns |
| Grazing | 1,9 | 3784.85*** | 1,9 | 2905.33*** |
| Freq. x grazing | 4,9 | 769.99*** | 4,6 | 596.71*** |
| R$^2$adj | 1 | 1 | 1 |

*: $0.01 < p \leq 0.05$; **: $0.001 < p \leq 0.01$; ***: $p \leq 0.001$; ns: not significant; DF (n,d) = degrees of freedom (nominator, denominator).

Figure 4. Change in mean ($\pm$SD) extinction probability in the *C. epithymum* metapopulation after a 100 yr simulation with increasing seed emigration for three different values of seed bank persistence. Each population is subjected to a rotational management of 15 yr. Only the results for short-lived perennials (0.10) are presented. Note the incremental change in levels of seed emigration.
fraction of 0.04

modelled intermediate management scenario with a patch population, corresponds with the occupancy fraction of 20% of all suitable patches occupied by a *C. epithymum* observed during the long-term study on heathlands, over a 100-yr period. The proportion of occupied patches mowing events is needed to ensure a viable metapopulation landscapes subjected to a mowing frequency difference between grazed and ungrazed treatment was found in between two consecutive mowing events see Table 2. No which are mown per year (log scaled). For corresponding periods between two consecutive mowing events see Figure 5. No difference between grazed and ungrazed treatment was found in landscapes subjected to a mowing frequency >10 mown patches yr⁻¹. Metapopulation viability size is set at 50 individuals (dash-dotted line).

relatively high patch turnover rates applied in our simulations, and to the inclusion of a persistent seed bank, which may reduce the effect of environmental stochasticity. Nonetheless, previous research revealed that at the population level, vegetative overwintering via haustoria makes *C. epithymum* far less sensitive to local environmental stochasticity and benefits population (re)establishment and successful reproduction shortly after management events (Meulebrouck et al. 2009). Overwintering of established individuals plays a far less important role for metapopulation viability and long-term survival than seed persistence and seed dispersal.

**Impact of different management scenarios**

Our results clearly indicate that extinction probabilities of *C. epithymum* metapopulations are significantly determined by the frequency at which a management event is applied. The data showed that for a short-lived perennial with moderate seed persistence and very low seed dispersal rates, a mowing frequency with <15 yr between two consecutive mowing events is needed to ensure a viable metapopulation over a 100-yr period. The proportion of occupied patches observed during the long-term study on heathlands, 55 ± 20% of all suitable patches occupied by a *C. epithymum* population, corresponds with the occupancy fraction of the modelled intermediate management scenario with a patch turnover rate between 15 and 10 yr, holding an occupancy fraction of 0.04 ± 0.01 and 0.84 ± 0.02, respectively. The results do not reveal any influence of spatial patch arrangement on metapopulation persistence, similar to these reported by Johst et al. (2002), who stressed that the rate of disturbance frequency in a landscape may be more important than spatial patch arrangement. Previous work on natural *C. epithymum* populations also showed no effect of patch size and/or spatial isolation on population size (Meulebrouck et al. 2007). In contrast with several other heathland species which do show an area and/or isolation effect (Piessens et al. 2004), *C. epithymum* can bridge some years of unsuitable conditions by its persistent seed bank. Seeds that arrive into such unsuitable heathland patches become a part of the soil seed bank. The capacity to form persistent soil seed banks may thus explain why spatial patch arrangement is much less important than management frequency for *C. epithymum* metapopulations.

Although *C. epithymum* metapopulations appeared to benefit from any management frequency with a mowing frequency lower than 15 yr, our results did demonstrate that an intermediate disturbance frequency generated the best conditions for metapopulation survival in the long-run, and that survival probabilities decreased again once a disturbance frequency threshold of 4 yr between two consecutive mowing events was exceeded. The latter can be attributed to the fact that *C. epithymum* needs sufficient young *C. vulgaris* individuals to guaranty establishment. When patches are managed too frequently, there is, however, not enough time for heather to grow back and reach a suitable size to be infested by *C. epithymum*. In that case, the suitable period is often too short for *C. epithymum* to establish and develop into a population that is capable to build up a viable seed bank via its reproductive output. Finally, extensive grazing caused a significantly higher metapopulation survival response and so would compensate for an inadequate mowing frequency. This may be explained by the constant presence of young heather plants that extensive grazing provides. The speed of vegetation succession reduces when heathland is grazed (Vandvik et al. 2005), making mown patches suitable for *C. epithymum* for a longer period than if there was no grazing.

**Conclusions**

Although it is generally assumed that early successional species invest in a persistent seed bank to buffer local extinction in continuously changing environments (Fenner and Thompson 2005), to our knowledge, this work is one of the first to demonstrate that the occurrence of seed banks in combination with occasional long-distance dispersal is necessary to ensure the metapopulation viability and long-term survival of an early successional species. If, however, emigration rates are too low, and/or the species fails to produce enough persistent seeds, a sufficiently high management frequency (time between two consecutive mowing events <15 yr) is needed to sustain a viable metapopulation of *C. epithymum*. Cessation of management, or very infrequent management events appear to be very harmful to this short-lived species, whereas extensive grazing can, at least partly, compensate for this lack of management. The results show that, in contrast to the current large-scale management applications on many heaths, the best techniques to maintain viable *C. epithymum* metapopulations are activities such as small-scale cyclical mowing, burning or turf-cutting, in combination with livestock grazing.

The methodology presented in this study is also applicable to other disturbed environments, e.g. flood-
fire-structured communities and semi-natural grasslands. The processes and interactions between life-history traits and management reported in this work will be relevant to metapopulations of many other plants and animals, which live in early successional vegetation. This study thus reveals that the metapopulation approaches used in this work is a useful tool to study plant population dynamics at a landscape scales, and indicates the need for incorporating both spatiotemporal aspects of patch suitability and demographic traits, especially seed persistence, in future metapopulation studies in dynamic landscapes.

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References


