Perspectives in Plant Ecology, Evolution and Systematics 12 (2010) 21–29

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.de/ppees

Research article

Reproductive success and pollen dispersal in urban populations of an insect-pollinated hay-meadow herb

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ARTICLE INFO

Article history:
Received 7 October 2006
Received in revised form
18 August 2009
Accepted 24 August 2009

Keywords:
Centaurea jacea
Connectivity
Fluorescent dye
Population size
Seed production
Urban parks

ABSTRACT

Urban development increasingly occupies more landscape and is responsible for habitat alteration and fragmentation of so many ecosystems that urban environments can no longer be excluded from the areas to be considered in conservation strategies. Appropriate management measures ensuring population viability are needed, but due to the usually irreversible feature of the urbanisation process, the measures may differ from non-urbanised areas. Sufficient gene flow levels, leading to successful seed production, appear to be a key element in the sustainable persistence of insect-pollinated plant remnant populations. This study investigated reproductive success and pollen dispersal patterns in *Centaurea jacea*, an insect-pollinated hay-meadow herb, in the Brussels urban area (Belgium). Reproductive performance of urban park populations was compared with populations occurring in urban semi-natural sites. Pollen dispersal patterns were examined within and among-population patches from two urban parks using fluorescent dye as a pollen analogue. Urban park populations showed a higher reproductive success than those in urban semi-natural sites. Depositions of fluorescent dye particles on recipient individuals were found within populations (<20 m), among populations within parks (over a few hundred meters) and among parks (maximal investigated distance: 2.6 km), indicating pollinator movements and a potential gene flow by pollen over relatively long distances. Dye dispersal showed an exponential decay distribution with respect to spatial distance. The very small populations received more immigrant dye deposition when located at short distances from the source population. These findings demonstrate that urban populations do not perform worse in reproductive success than populations from agricultural landscapes, despite their small size, and can function as a network exchanging pollen. The conversion of urban park lawns into interconnected networks of ecologically managed hay meadows, allowing simultaneous flowering and seed production in many patches of target species, is to be strongly encouraged.

Introduction

In many countries urban areas increasingly occupy more land and are responsible for habitat alteration and fragmentation of so many ecosystems that urban environments can no longer be ignored in conservation strategies. Indeed, besides the fact that they can still maintain some biodiversity, it appears crucial to avoid urban settings becoming an uninhabitable zone for wild species and to become barriers impeding species dispersal, especially in the context of climate change and of the development of the European Natura 2000 Network, which aims at favouring species migration (McKinney, 2002; Lawson et al., 2008; Lundberg et al., 2008; Mcdonald et al., 2008; Kadlec et al., 2008; Williams et al., 2009).

Urban pressure is particularly high for plant species. As land is needed for the construction of buildings and roads, habitat fragmentation is extreme, and usually irreversible. Plant habitats within urban areas can be considered as semi-natural. That is to say, these are wild habitats modified by human activity but still holding species that naturally occur in the area and showing dynamics primarily determined by natural processes. These semi-natural habitats persist as small isolated remnants, embedded in a hostile human-used matrix but also incurring anthropogenic pressure, e.g. artificialisation, recreational activities, and increased pollution and eutrophication (Godefroid, 2001; McKinney, 2002; Guirado et al., 2006; Williams et al., 2009). Therefore, many species, even common ones, often occur as small, isolated populations (Ewers and Didham, 2006; Van Rossum, 2008). These populations are expected to be affected by demographic, environmental and genetic stochasticity, show pollination failure and disrupted gene flow processes and incur edge effects. The main

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doi:10.1016/j.ppees.2009.08.002

consequences can be expressed as low demographic performance, reduced reproductive success, genetic erosion, inbreeding depression and reduced dispersal capabilities (e.g. Kwak et al., 1998; Soons and Heil, 2002; Oostermeijer et al., 2003; Aguilar et al., 2006). Through these processes, populations may have reduced potential to respond to environmental changes, higher vulnerability to competition and environmental stresses such as invasive exotics, pest, diseases and pollution, and increased extinction risk (Young et al., 1996; Bowman et al., 2008). So even if habitat restoration through ecological management can lead to higher habitat quality and to short-term increase of biodiversity in urban habitats, survival of populations may be compromised in the long term, due to these demographic and genetic processes (Vergeer et al., 2003; Volis et al., 2005; Lundberg et al., 2008; Van Geert et al., 2008; Van Rossum, 2008; Rusterholz et al., 2009). Appropriate management measures ensuring population viability are essential, but due to the usually irreversible feature of the urbanisation process, the measures may differ from those in non-urbanised areas. For instance, it is often impossible to recreate large areas of continuous wild habitats.

Sufficient gene flow levels within and among remnants, leading to successful seed and seedling production, appear to be a key element in the sustainable persistence of insect-pollinated plant populations (Ellstrand, 1992; Richards, 2000; Wilcock and Neiland, 2002; Volis et al., 2005). For many plant species, seed dispersal is restricted and gene flow is mainly assumed by pollen dispersal (e.g. Levin and Kerster, 1974; Vekemans and Hardy, 2004). In insect-pollinated plant species, pollen dispersal within and between populations primarily depends on pollinator type, abundance and foraging strategies (e.g. Inouye et al., 1994; Cresswell et al., 1995; Richards, 1997). Pollinator efficiency and foraging behaviour can be influenced by several, often-interacting factors, such as spatial isolation of individual plants and populations, plant population demographic traits (population size, plant density), heterospecific flowering species richness and the size of floral display (e.g. Kunin, 1997; Kwak et al., 1998; Schulke and Waser, 2001). Pollination processes and reproductive performance of insect-pollinated plant species have been thoroughly investigated when habitat fragmentation results from the intensification of agricultural practices (e.g. Steffan-Dewenter and Tscharntke, 1999; Steffan-Dewenter et al., 2001; Brys et al., 2003; Hirsch et al., 2003; Oostermeijer et al., 2003; Van Rossum and Triest, 2003). In contrast, fewer studies have evaluated reproductive success, pollen dispersal patterns and connectivity by pollen flow in fragmented insect-pollinated plant populations in an urban setting (Roberts et al., 2007; Rusterholz et al., 2009; Van Rossum, 2009). Yet, pollinator service and abundance may differ in farmland and urban landscapes (Goulson et al., 2002, 2008; Chapman et al., 2003; Tommasi et al., 2004), which might lead to different response patterns of plant populations to habitat fragmentation.

The present study investigated pollen dispersal patterns and reproductive success of the insect-pollinated herb *Centaurea jacea* (Asteraceae) in Brussels urban area (Belgium). In Brussels, *C. jacea* is relatively rare and shows a fragmented distribution (Allemeersch, 2006). Its populations occur in hay-meadow remnants, in semi-natural sites, but also in parks, especially those where specific ecological management has been applied for more than a decade in order to restore native vegetation areas. Restored patches of hay-meadow vegetation have been created through mowing only once or twice a year and the plants they contain spontaneously occur (Hannequart and Schamp, 1999). However, these patches are often small ($< 1000\,m^2$), and show a highly fragmented structure among but also within parks. Populations from urban semi-natural sites and parks were examined for their reproductive components. Fluorescent powdered dye was used to track pollinator movements and estimate the spatial patterns of pollen dispersal within and among-population patches from urban parks. Fluorescent dye can be considered as a good analogue of pollen when pollinators are insects, such as Hymenoptera (bees, bumblebees), Lepidoptera (butterflies and moths) and Diptera (e.g. Kearns and Inouye, 1993; Rademaker et al., 1997; Young, 2002; Gaudeul and Till-Bottraud, 2004; Adler and Irwin, 2006; Van Rossum, 2009). The following questions were addressed: (1) What is the reproductive performance of *C. jacea* in urban populations, and do park and semi-natural site populations differ in their reproductive success? (2) What are the patterns of pollen dispersal (using dye as pollen analogue) within and between populations in urban parks? Whether urban hay-meadow patches might sustain viable plant populations through pollen flow connectivity is discussed.

Materials and methods

The species

C. jacea L. *sensu lato* (knapweed, Asteraceae) is a hermaphroditic, self-incompatible, long-lived perennial herb that is widespread throughout Europe. It typically occurs in mesophilous grassland and hay-meadow (*Arrhenatherion*) habitats. Flowering is protandric and occurs in June–August. Flower stalks reach heights of 20–90 cm. Capitula (flower heads) contain approximately 40 purple flowers on the central disc and a ring of sterile ray flowers may be present (Hardy and Vekemans, 2001). Pollination is mediated by insects, mainly Hymenoptera (solitary bees, honeybees and bumblebees), Lepidoptera and Diptera (Syrphidae) (Steffan-Dewenter et al., 2001; Hirsch et al., 2003). Field observations indicated that insect visitors were mainly bumblebees (e.g. *Bombus lapidarius*, *Bombus pascuorum* and *Bombus terrestris*), honeybees and solitary bees, hoverflies and Lepidoptera (Van Rossum, personal observations). Plants reproduce only by seeds (as achenes), which can form a transient seed bank (Thompson et al., 1997). Achenes, which may have a small pappus, are dispersed over short distances by gravity and wind (Soons and Heil, 2002). In Belgium, *C. jacea* is a common species (Van Rompaey and Delvosalle, 1979), but it is relatively rare in the Brussels Capital Region (Schamp and Hannequart, 1999; Allemeersch, 2006).

Study site and populations

The Brussels Capital Region (4°22′E 50°50′N, 163 km^2; 1 million inhabitants) corresponds to the wider urban area of Brussels (which also encompasses more rural suburbs). It comprises many entirely man-made green spaces (parks, cemeteries; Fig. 1), but also a number of semi-natural sites, some of which are protected as nature reserves (Hannequart and Schamp, 1999). Field surveys were conducted from the beginning of June 2004 in the Brussels area, mainly based on former detailed inventories (Schamp and Hannequart, 1999; Godefroid, 2001) and on excursion reports from the Brussels floristic group of the Floristic Study Association (AEF). Fifteen urban patches of individuals of *C. jacea*, hereafter called "populations", were found back (Fig. 1); some formerly known locations had disappeared. Three populations were not included in the study; two populations were already mown and one had only one flowering individual. Out of the 12 studied populations, eight occurred in ecologically managed hay-meadow remnants (mown once or twice a year) or lawns in parks and four occurred in meadows of semi-natural sites (Table 1). All populations are natural (not sown) (Godefroid, 2001). Except for