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Timing of mowing influences genetic diversity and reproductive success in endangered semi-natural grassland plants

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ABSTRACT

Recent global land-use changes have led to reductions in many herbaceous plant species in semi-natural grassland landscapes. Changes in management frequency and intensity are known to cause declines in plant populations. However, little is known about the impact of changes in the timing of management practices on the genetic diversity as well as the reproductive success of rare semi-natural grassland species. We determined the suitable management (mowing) timing for *Vincetoxicum pycnostelma* Kitag. (Apocynaceae; Asclepiadoideae), an endangered summer- and autumn-blooming semi-natural grassland herb. We examined 15 *V. pycnostelma* populations to assess the effects of mowing timing on the genetic diversity of each population using nine microsatellite markers and on pollination and reproductive success. Pollination success was not affected by flowering timing. Mowing during the mid- to late flowering and fruiting periods of *V. pycnostelma* (July–September) had a significant negative effect on the number of inflorescences and total fruits produced, whereas mowing before flowering and growing periods (April, May and November–March) had positive effects on the number of inflorescences and fruits, respectively. Furthermore, mowing during the mid- to late flowering and fruiting periods also caused a significant decrease in genetic diversity. Our results demonstrated that mowing events during the mid- to late flowering and fruiting periods caused significant declines in the genetic diversity and/or reproductive success of *V. pycnostelma*. By contrast, mowing before flowering periods significantly enhanced reproductive success. To conserve semi-natural grassland herb diversity, mowing should be avoided during seasons when the flowering and fruiting periods of many endangered species overlap.

1. Introduction

In recent decades, the area and biodiversity of semi-natural grasslands within agricultural landscapes have been globally and rapidly decreasing because of drastic changes in traditional and extensive land-use systems, garnering much attention from basic and applied ecologists (IUCN, 2012; Kleijn et al., 2011; Krebs et al., 1999; McNeely et al., 1995; Tilman et al., 2001; Tscharntke et al., 2005). Together with recent changes in anthropogenic disturbance (e.g., mowing, burning, and grazing) regimes, abandonments of threatened semi-natural habitats, which have been caused by degradation and conversion of rural life styles and cultures, have decreased plant diversity, particularly the number of rare endangered species in European and Asian semi-natural grasslands (Albrecht and Haider, 2013; Babai and Molnár, 2014; Kleijn et al., 2011; Uchida and Ushimaru, 2014; Uematsu and Ushimaru, 2013).

Although several studies have elucidated the negative impacts of both increases and decreases in disturbance frequency and/or intensity on semi-natural grassland plant diversity (Ekroos et al., 2010; Kleijn et al., 2011; Pöyry et al., 2006; Uchida and Ushimaru, 2014; Uematsu et al., 2010), little is known about the effects of changes in the timing of management practices on plant diversity and the reproductive success of individual plant species (Brys et al., 2004; Endels et al., 2007). Because plant species usually exhibit seasonal reproductive activity (i.e., flowering and fruiting), anthropogenic disturbances during flowering and fruiting periods tend to diminish reproductive success (Brys et al., 2004; Endels et al., 2007; Jantunen et al., 2007). If semi-natural grassland plants have adapted their reproductive periods to traditional management timing, changes in these timings may also negatively impact plant fitness via a reduction in seed production.

The above hypothesis has been tested by several researchers (Brys et al., 2004; Endels et al., 2007; Jantunen et al., 2007); however, the process by which changes in management timings

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cause declines in populations has not been sufficiently examined for plants living within agricultural landscapes. Anthropogenic disturbances during the reproductive period of animal-pollinated flowers may diminish seed production in several ways. The first is a basic reduction in the number of reproductive units. Mowing during flowering and fruiting periods inevitably reduces the numbers of flowers and fruits (Brys et al., 2004; Endels et al., 2007; Jantunen et al., 2007), leading to reduction in seed sets. Second, a reduction flower number results in decreased pollination success. Because both individual- and population-level numbers play important roles in pollinator attraction (Ebeling et al., 2008; Potts et al., 2006), a reduction in flower number can result in lower seed production in both respects. Furthermore, pollinator abundance and richness could be decreased by changes in disturbance regimes, independent of flower reduction (Hudewenz et al., 2012; Kearns et al., 1998; Söderström et al., 2001). Thus, to determine the effects of changes in disturbance regime on reproductive success in animal-pollinated plants, these scenarios should be examined simultaneously.

Natural and anthropogenic disturbance regimes can also affect genetic diversity in plant populations (Marchi et al., 2013; Rüdinger et al., 2008). Genetic diversity within a given population is considered important for the conservation of endangered plant species, as genetic diversity is usually positively correlated with fitness: low genetic diversity within a population greatly diminishes fitness through inbreeding depression and qualitative pollen limitation, particularly in self-incompatible species (Johansson et al., 2007; Leimu et al., 2006; Young and Pickup, 2010). Reduced seed recruitment due to mowing and grazing during the annual reproductive period may lower genetic diversity in small and isolated populations. Thus, changes in management practices can cause local extinction of species through a loss of genetic diversity. However, the effects of the timing of management practices on genetic diversity in semi-natural grassland plants have rarely been investigated and remain unclear.

In the present study, we examined the reproductive success and genetic diversity of 15 *Vincetoxicum pycnostelma* Kitag. (Apocynaceae; Asclepiadoideae) populations subjected to different management practices maintained for at least last 10 years. Using this endangered perennial herb species as the study subject, we aimed to elucidate the impact of the timing of an anthropogenic disturbance (mowing) on the sexual reproduction and genetic diversity of a semi-natural grassland plant. Although this species was very common in the region a few decades ago, it has experienced rapid population declines due to changes in land-use in semi-natural grasslands throughout Japan (Environment Agency of Japan, 2000; Uematsu et al., 2010). *V. pycnostelma* is a representative example of many native herbaceous plants that reproduce from summer to autumn but that have rapidly declined in semi-natural grasslands (Koyanagi and Furukawa, 2013). Assessing the effects of mowing timing is also essential for planning the conservation of endangered semi-natural grassland herbs as well as entire plant communities. We predict that intensive mowing during their flowering and fruiting periods will significantly reduce not only reproductive success but also the genetic diversity of this endangered grassland species. Based on our results, we discuss the importance of traditional management practices and suitable management timings for the conservation of semi-natural grasslands and the diversity of endangered plants, including *V. pycnostelma*.

2. Materials and methods

2.1. Study species

V. pycnostelma is a perennial herb species endemic to the semi-natural grasslands of Japan, Korea, China, and Russia (Kitamura et al., 1957). The flowers of *V. pycnostelma* produce pollinia, which have a sticky appendage called a corpusculum. The flowers are self-incompatible and open at night, and small- and intermediate-sized moths (Lepidoptera) and crane flies are recorded as pollinators (Nakahama et al., 2013a,b; Yamashiro et al., 2008). Relatively large follicle fruits (7 mm in diameter, 5–7 cm in length, including several tens of seeds) mature during September to October. The life-form of the species is geophyte, based on Raunkiaer (1934): rhizomes have many shoot meristems so that above-ground shoots can quickly regrow even after mowing. During recent decades, this species has experienced rapid population declines due to natural

Table 1
Characteristics of the fifteen *V. pycnostelma* populations examined in this study. Population ID, area (m^2), population size, the mean vegetation height, and mowing practice (the presence or absence of the mowing event during the each period and total number of mowing events per one year) are indicated for each population. Mowing timings were divided into five groups depending on mowing practice (see text for details). Selective mowing is indicated as 0.5.

ID	Prefecture	Area (m^2)	Population size	Mean vegetation height (cm)	Mowing events					Total number of mowing events per one year
					Pre growing period	Growing period	Early flowering period	Flowering peak	Late flowering and fruiting period	
					(November–March)	(April, May)	(June)	(July)	(August, September)	
a	Gifu	67.3	92	9.58	0	0	0	1	0	1
b	Aichi	333.3	260	54.17	1	0	1	0	0	2
c	Shiga	1486.7	300	60.83	1	0	1	0	0	2
d	Osaka	320.0	220	12.92	0	0	1	0	1	2
e	Osaka	154.18	100	31.67	0	0	0	0	1	1
f	Hyogo	277.73	180	66.25	1	1	0.5	0	0.5	4
g	Hyogo	200.48	200	40.83	0	0	1	0	0	1
h	Hyogo	180.06	42	38.75	0	0	0	0	0.5	2
i	Hyogo	332.48	58	43.75	0	0	1	1[a]	0	1
j	Hyogo	75.0	5	34.58	0	1	0	1	0	2
k	Hyogo	430.6	24	38.75	1	1	1	0	1	4
l	Hyogo	340.9	30	86.25	1	0	0	0	0	l
m	Hyogo	237.6	100	43.33	1	1	1	0	1 + 0.5	5
n	Hyogo	823.0	60	52.5	1	0	0	0	0	1
o	Hyogo	753.9	50	34.17	1	0	0	1(0.5[b])	0	3

[a] Prior to 2010, population i was mowed in July (in italic) unlike recent mowing practices that take place in June.
[b] Prior to 2011, population o was selectively mowed in July (in italic).