



Clonal growth buffers the effect of grazing management on the population growth rate of a perennial grassland herb



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ABSTRACT

Grazing is an important management action to conserve biodiversity in semi-natural grasslands but it is important to understand how grazing influences the life-history components and population dynamics of plant species. In this study, we analysed effects of grazing intensity and abandonment on population dynamics of the semi-natural grassland species *Knautia arvensis* which is an important nectar source for pollinating species and an indicator of biodiversity in agricultural landscapes. We recorded life-history stage, survival, establishment of seedlings and ramets, number of inflorescences and grazing marks on permanently marked individuals in eight populations in mid-Norway for three consecutive years. Matrix modelling was used to estimate population growth rates and elasticities, and life Table response experiments (LTREs) were used to assess the contribution of different life-history components to the observed variation in population growth rates between different management treatments. Generalized linear mixed effects models (GLMMs) were used to investigate the effect of management on vital rates and number of inflorescences as well as damage to *K. arvensis* individuals. Populations in abandoned grasslands had more inflorescences, a lower proportion of seedlings and a higher proportion of flowering ramets compared to populations in grasslands under high grazing intensity. There were no differences in population growth rates between different grazing intensities. Fecundity however, contributed more to the growth rate in grazed grasslands compared to abandoned grasslands where clonal regeneration contributed the most. Survival of non-flowering rosettes made the largest impact to overall growth rates. Our results indicate that a long life-span and clonal growth buffer the effect of environmental change in abandoned grasslands and that there is a trade-off between fertility and clonal regeneration in *K. arvensis* populations.

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1. Introduction

Semi-natural grasslands harbour a high diversity of plant species (Marini et al., 2008). However, the area of semi-natural grasslands in Europe has decreased due to agricultural intensification, changed management practices and abandonment (Hodgson et al., 2005; Poschlod and WallisDeVries, 2002). Semi-natural grasslands that have been abandoned or managed at too low intensity to halt successional change will gradually be invaded by shrubs and trees (Wehn, 2009). As a result, growth conditions become less favourable for light-demanding species in particular (Pykala et al., 2005), and populations of such species may rapidly decline once

grasslands have been abandoned (Endels et al., 2007b; Hamre et al., 2010).

Extensive grazing is recommended as a management tool to maintain or improve plant population viability in semi-natural grasslands (Metera et al., 2010; Wrage et al., 2011). Herbivory affects plant abundance and distribution as well as plant traits (Louault et al., 2005; Maron and Crone, 2006). Effects of grazing on plant performance are both direct and indirect; indirect through changing the habitat quality by trampling, reducing competition, addition of nutrient and litter accumulation (Brys et al., 2004; Ehrlén et al., 2005) and direct by damaging the plant or reducing flowering and seed set (Knight, 2004). Hence, different levels of grazing intensity can have disparate effects on vital rates and the demographic behaviour of plant populations (Brys et al., 2004; Lennartsson and Oostermeijer, 2001). Vital rates may even differ between populations of a single species, depending on grazing intensity and the time since abandonment (Brys et al., 2004; Jacquemyn and Brys, 2008). The life span of a species may correlate

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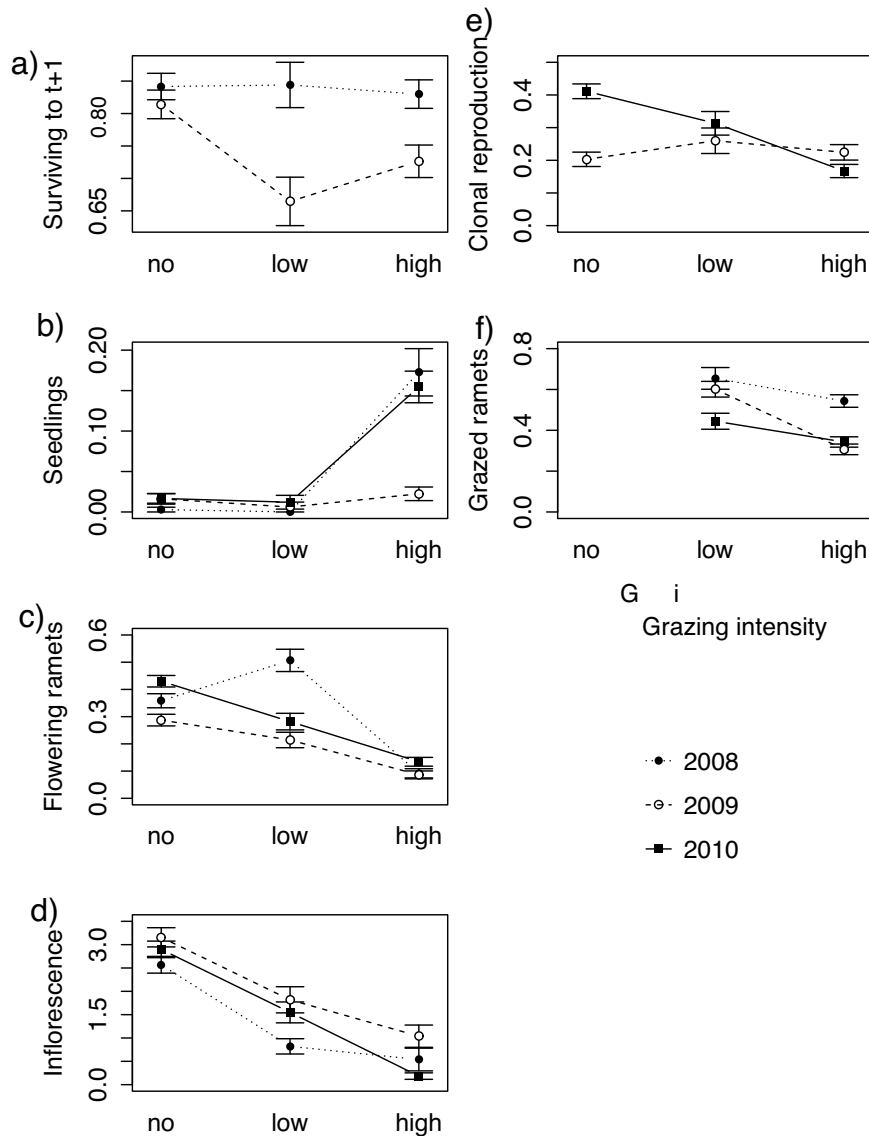


Fig. 1. Mean and standard error of (a) survival to the next year ($t+1$), (b) proportion of seedlings, (c) proportion of flowering ramets, (d) number of inflorescences per ramet, (e) proportion of clonal reproduction, and (f) proportion of grazed ramets in *Knautia arvensis* populations in 2008, 2009 and 2010 in semi-natural grasslands with no (abandoned), low and high grazing intensity.

with its population dynamics, and longevity can buffer changing environmental conditions (Morris et al., 2008). Long-lived perennial plants are known to have more stable population sizes than short-lived plants, because in general survival has less variability than fecundity, and fecundity is relatively more important for population dynamics of short-lived plant species (Garcia et al., 2008). Because grazing affects different life-history stages simultaneously, it is essential to integrate multiple vital rates within a single analysis to fully understand the population dynamics and viability of a species. In stage-structured populations this can be achieved using matrix models (Caswell, 2001).

The objective of this study is to analyse the effect of grazing intensity and abandonment on population dynamics of the clonal species *Knautia arvensis*. We want to estimate how its life-history components contribute to its population growth rate in semi-natural grasslands under different land-use regimes. In Norway, *K. arvensis* can be regarded as a keystone species upholding species richness in semi-natural grasslands as it is an important nectar source for many species of butterflies, bumblebees, solitary bees and other groups of pollinating insects, e.g. the Norwegian red

listed mining bee *Andrena hattorfiana* (Cahenzli and Erhardt, 2012; Clausen et al., 2001; Franzen and Nilsson, 2008; Kålås et al., 2010; Totland et al., 2013). Models were developed to assess how abandonment and different levels of grazing intensity by cattle influence plant traits, vital rates, life-history components and growth rate. The contribution of vital rates to the growth rate for each level of grazing intensity was determined to see whether *K. arvensis* had different reproduction strategies when exposed to different levels of herbivory.

2. Methods

2.1. Study species

Knautia arvensis (L.) Coult. is a perennial, clonal herb with a generalist pollination system that grows in grasslands, open woods, on road verges and ruderal sites. The species is widely distributed in Europe, west Asia and north-west Africa (Lid and Lid, 2005). It has a sympodial, branched stock with leaf rosettes and flowering stems, a taproot and usually lateral underground rhizomes (Tutin

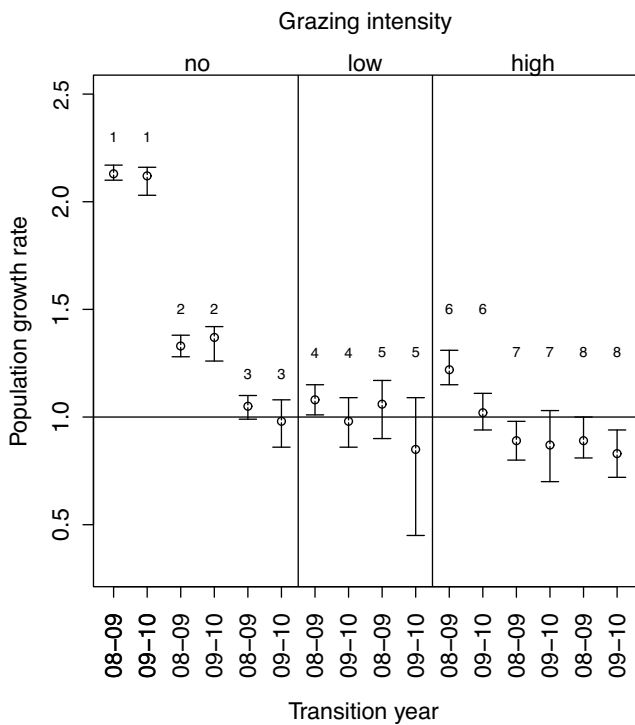


Fig. 2. Projected population growth rates for *Knautia arvensis* populations (1–8) in semi-natural grasslands with no (abandoned), low and high grazing intensity in two transition years (2008–2009 and 2009–2010). The error bars are bootstrapped 95% confidence intervals.

et al., 1976). According to Thompson et al. (1997) *K. arvensis* has no persistent seedbank. The species is able to germinate under a wide range of environmental conditions (Vandvik and Vange, 2003). However, early seedling establishment has been found to be poor in closed grassland vegetation but positively affected by disturbance that creates tiny gaps with bare soil (Hovstad, 2007). Larsson (2005) found *K. arvensis* to have a mean of 6.7 inflorescences per fertile ramet and mean number of flowers per inflorescence to be 67.1. In the present study we measured a mean of 29 seeds per inflorescence.

2.2. Study area

The study area is located in mid-Norway (Nord-Trøndelag county) and covers an area of 20 km² (UTM 618650E, 7070496 N) and the elevation ranges from 80 to 180 m asl. Mean annual temperature is 4.7 °C and mean annual precipitation is 815 mm in the study area (normal period 1961–1990) (Norwegian Meteorological Institute, 2014). The study area is in the middle and southern boreal vegetation zones, in the slightly oceanic vegetation section (Moen, 1999), and the bedrock consists mainly of shale and some mica schist (data provided by Geological Survey of Norway NGU, 2014). In this study we refer to semi-natural grasslands as grasslands with a long and continuous extensive management (grazing or mowing) where species have not been sown or planted. In the studied grasslands there were no canopies of woody species, and the compositions of plant species had not been altered significantly by use of fertilizers or herbicides (Norderhaug et al., 2000).

2.3. Study design and data collection

All semi-natural grasslands in the study area were surveyed in 2008 and presence/absence of *K. arvensis* was recorded. From this survey, eight semi-natural grassland sites of at least 0.2 ha were

selected. Neither population size nor viability of *K. arvensis* were used as criteria for the selection of sites. Three of the grasslands were abandoned (8–15 years ago) and five were grazed. The intensity of the grazing in the grazed grasslands was a result of the farmer's practice and not set by the study. Information about the management of the grasslands were achieved by semi-structured interviews with the farmers. Grazing took place throughout the grazing season (May–September), but were regulated in a non-structural way. The farmers had access to several grasslands. In all grazed sites, livestock were taken on and off the grassland several times throughout the grazing season and some grasslands were preferred and managed more intensively. In the preferred grasslands the livestock were taken off the grasslands when sward height became less than 4–8 cm. The less preferred grasslands were then used as offset areas. In general, the offsets had a higher stocking rate in late summer, compared to spring and early summer. We did not control the number of animals per unit area but based on the qualitative data provided by the interviews, we divided the grazed grasslands into two classes of grazing intensities: low grazing intensity (n = 2; the offsets) and high grazing intensity (n = 3; the preferred grassland). In the grasslands defined as under high grazing intensity, the mean vegetation height over at least 75% of the area was <4–8 cm, and in grasslands defined as under low grazing intensity the vegetation height was >20 cm in mid-July. Generally, in the less preferred grassland (under low grazing intensity) some of the vegetation was left ungrazed by the animals. In the abandoned grasslands there was no encroachment as yet. All grasslands were situated on a hillside facing south–south-west and had approximately similar slopes and there were no overgrazing or large areas of bare soil due to animal trampling.

In 2008, study plots of 1 m × 1 m were established randomly within each of the selected semi-natural grasslands. Nine to 14 study plots with *K. arvensis* and two study plots without *K. arvensis* were established and permanently marked within each grassland. Study plots without *K. arvensis* were selected in order to record the establishment of new individuals. Within each plot, all ramets of *K. arvensis* were permanently marked. A total of 72 plots and 1454 ramets were included in the study. Each summer, 2008–2010, a census of the study species within all plots was conducted and for each ramet survival, evidence of grazing, number of inflorescences per ramet, and life-history stage were recorded. In addition, establishment of seedlings and clonal ramets were recorded within each plot. We distinguished five life-history stages for *K. arvensis*: seedlings, non-flowering clonal offspring, flowering clonal offspring, non-flowering rosette and flowering rosette. Seedlings were defined as small plants younger than one year old. New individuals in the plots were marked and included in the study at each census.

2.4. Statistical analysis

The effect of management and temporal variation on the number of inflorescences per ramet, vital rates (survival to the next year, proportion of flowering ramets, proportion of seedlings and flowering and non-flowering clonal offspring) and proportion of grazed ramets in each plot were analysed using a generalised linear mixed effects model (GLMM). Ramet ID, plot and grassland were included as nested random factors in the models. Year and grazing management were included as fixed factors. The random, nested sampling structure was included to avoid problems with pseudoreplication. The response variables were modelled using a binomial distribution, except for number of inflorescences where a Poisson distribution was used. Models were made sequentially and reduced by backward elimination of non-significant fixed effects (α defined as 0.01; Crawley, 2007; Zuur, 2009). The estimates and statistics presented are from the final reduced models for each response variable.

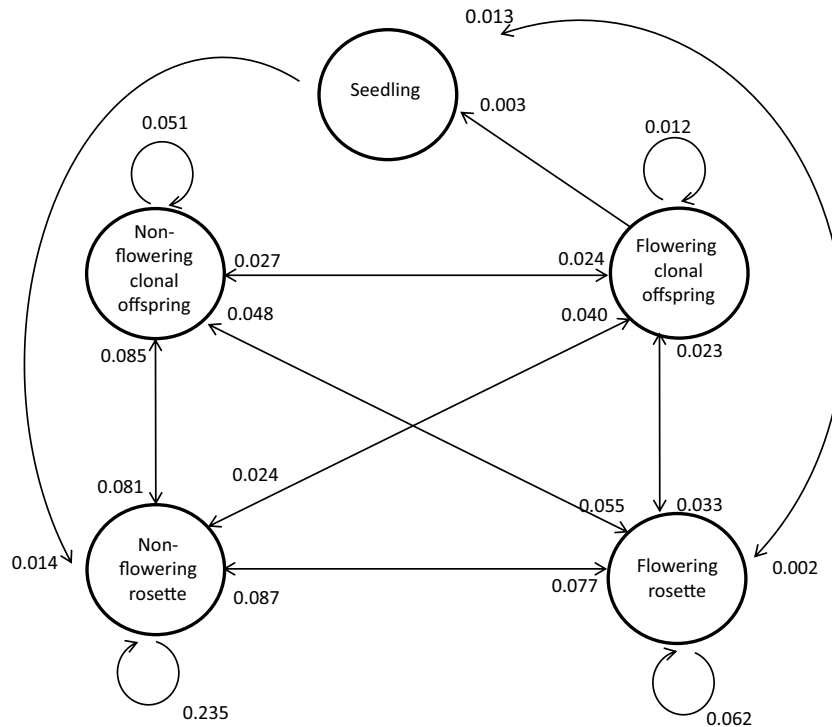


Fig. 3. Life-cycle of *Knautia arvensis* covering five stages. The arrows represent yearly transitions and elasticity values of the overall mean matrix are given.

Table 1
Transition matrix model for *Knautia arvensis* with five stage classes: seedlings, non-flowering clonal offspring, flowering clonal offspring, non-flowering rosette and flowering rosette. Transitions are grouped according to seven life-history components: clonal reproduction (CR), fecundity (F), survival of clonal offspring (SC), seedling survival (SS), stasis (S), retrogression (R) and entering flowering stage (EF). “0” indicates that there are no transitions between the stage classes. Subscript numbers by the matrix elements indicate the transitions from stage j to i in one-year intervals ($t+1$).

		year t				
		Seedlings	Non-flowering clonal offspring	Flowering clonal offspring	Non-flowering rosette	Flowering rosette
year t + 1	Seedlings	0	0	F ₁₃	0	F ₁₅
	Non-flowering clonal offspring	0	CR ₂₂	CR ₂₃	CR ₂₄	CR ₂₅
	Flowering clonal offspring	0	CR ₃₂	CR ₃₃	CR ₃₄	CR ₃₅
	Non-flowering rosette	SS ₄₁	SC ₄₂	SC ₄₃	S ₄₄	R ₄₅
	Flowering rosette	SS ₅₁	SC ₅₂	SC ₅₃	EF ₅₄	S ₅₅

The demographic data were analysed by constructing stage-classified population matrix modelling (Caswell, 2001) with a 5×5 projection matrix for each year-to-year transition (Table 1). The transition matrix model was in the form:

$$n_{(t+1)} = An_{(t)},$$

where A is a population projection matrix containing the transition probabilities between stages or stage-specific fecundity, $n_{(t)}$ is a vector of stage-classified individuals at time t , and $n_{(t+1)}$ is the vector of stage-classified individuals at time $t+1$.

All possible transitions are described in Table 1. Transitions were grouped according to seven life-history components: clonal reproduction, fecundity, survival of clonal offspring, survival of seedlings, stasis, retrogression and entering flowering stage. Retrogression is the transition from flowering to non-flowering stage, and entering flowering stage is the transition from non-flowering rosette to flowering stage. Since the species has no persistent seedbank (Thompson et al., 1997), no seed stage was modelled. In total, 16 projection matrices were constructed; one per population per year interval in addition to an overall mean matrix. For each transition matrix the projected population growth rate (λ) was estimated as the dominant eigenvalue of the matrix, in addition to the elasticity (proportional sensitivity) of the eigenvalues to changes in the vital

rates. The elasticity is an estimate of the relative contribution of a life-cycle transition to the projected population growth rate (λ ; Caswell, 2001).

Sexual fecundity was calculated as the estimated mean number of inflorescences per ramet multiplied by estimated number of seedlings in the population divided by inflorescences in the population (Brys et al., 2004). It was not possible to determine from which parent a ramet (=clonal offspring) had emerged without excavating underground rhizomes. Therefore clonal reproduction was estimated from the numbers of clonal offspring and flowering clonal offspring in year $t+1$ divided by the number of potential clonal offspring producers in year t (Berg, 2002). We assumed that all life-history stages except seedlings produced clonal offspring and that the transitions representing clonal reproduction were similar for all stages. When the study started it was not possible to know which ramets were new clonal offspring that year, and hence survival of non-flowering clones and flowering clones could not be estimated. The first annual transition (2008–2009) for non-flowering clones and flowering clones was therefore estimated using the next annual transition (2009–2010).

An analysis of a life Table response experiment (LTRE) was used to estimate the relative importance of grazing level, year and populations on the variation in λ (Caswell, 2001); a nested factorial

design was used (Elder and Doak, 2006; Endels et al., 2007a) and a LTRE linear model including grazing level (i), yearly transition (j), and populations nested within i ($l(i)$):

$$\lambda_{(ij)} = \lambda^{(\cdot)} + \alpha^{(i)} + \beta^{(j)} + \alpha\beta^{(ij)} + \theta^{(i)},$$

where $\lambda^{(\cdot)}$ is the projected population growth rate of the mean reference matrix, $\alpha^{(i)}$ and $\beta^{(j)}$ are the main effects, α = grazing intensity effect and β = year effects at the i^{th} level of grazing and the j^{th} level of yearly transition, $\alpha\beta^{(ij)}$ is the interaction effect and $\theta^{(i)}$ correspond to the nested effects of population l within grazing level i . Estimates of the treatments effects and decomposition into contributions from each matrix element were done as described in Caswell (2001) and Elder and Doak (2006). To investigate the importance of the different life-history components to differences in population growth rate, we separately summed all positive and negative contributions from the matrix elements within a life-history component. To estimate 95% confidence intervals for the growth rates and LTRE effects we used a bootstrapping procedure with 3000 resamplings (Caswell, 2001). The effect of management and temporal variation on the growth rates estimated from the matrix model, and the variation in growth rates among populations were also analysed using GLMM and the same backward elimination procedures as described above.

All statistical analyses were performed in R (R Core Team, 2013). The linear models were implemented using the lmer function in the lme4 package (Bates et al., 2015). The matrix modelling procedures and LTRE linear model were conducted using the package popbio (Stubben and Milligan, 2007).

3. Results

The numbers of inflorescences per ramet and proportion of flowering ramets in *K. arvensis* populations were highest in abandoned grasslands (mean \pm SE inflorescences: 2.88 ± 0.082 , $p < 0.05$; mean \pm SE flowering ramets: 0.36 ± 0.008 , $p < 0.05$) and lowest in grasslands with high grazing intensity (mean \pm SE inflorescences: 0.45 ± 0.030 , $p < 0.05$; mean \pm SE flowering ramets: 0.11 ± 0.005 , $p < 0.05$). The proportion of seedlings was greater in populations under high grazing intensity (mean \pm SE seedlings: 0.11 ± 0.005 , $p < 0.05$), except in 2009. Grazing intensity did not influence ramet survival but survival was lower in 2009 (mean \pm SE survival: 0.78 ± 0.011 , $p < 0.05$) than in 2008 (mean \pm SE survival: 0.84 ± 0.009 , $p < 0.05$). The effect of grazing intensity on the proportion of clonal reproduction (flowering and non-flowering clonal rosettes) and grazed ramets varied greatly between years and there were no overall trends but significant interaction effects between year and grazing intensity (interaction effects: $p < 0.05$; Table 2; Fig. 1).

The projected population growth rate (λ) ranged from 0.83 to 2.13 indicating that populations both increased and decreased in size. Elasticity analysis of the overall mean transition matrix indicated that the survival of non-flowering rosettes was the life-cycle transition that had the largest impact (elasticity = 0.235) on the projected population growth rate (Fig. 3). The population growth rate varied significantly among years ($\chi^2 = 5.35$, $p = 0.02$) with the highest growth rates in 2008–2009. The λ did not vary with grazing level ($\chi^2 = 4.28$, $p = 0.12$; Fig. 2). The growth rates varied among populations under no ($\chi^2 = 19.74$, $p < 0.01$) and high ($\chi^2 = 4.87$, $p = 0.02$) grazing intensity, but not among populations in grasslands under low grazing intensity ($\chi^2 = 0.76$, $p = 0.39$). Population 1 (no grazing intensity) had the highest growth rate (2.13). *K. arvensis* did not establish in the control plots where the species was absent in 2008.

The LTRE analysis revealed that the main effect of grazing intensity (mean \pm SD effect: $|0.201 \pm 0.103|$) contributed more to variation in population growth rate than both year

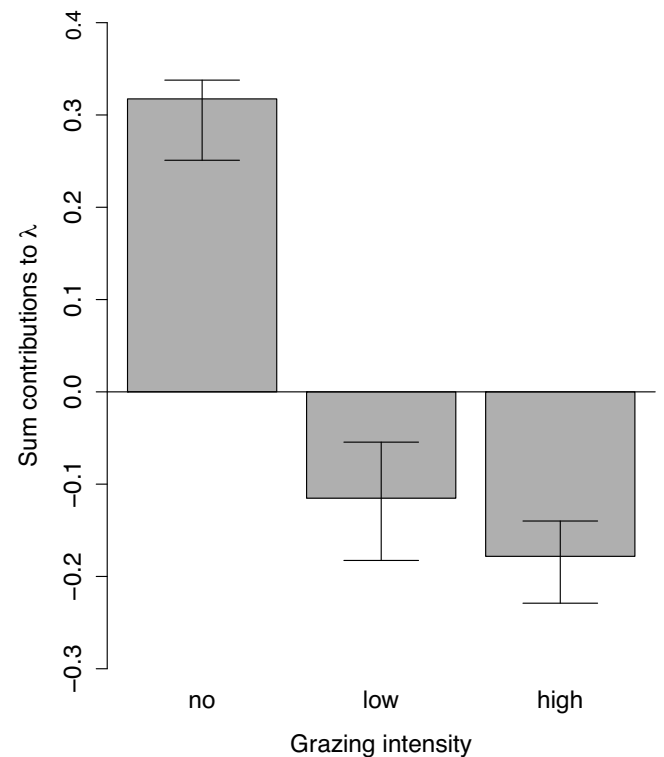


Fig. 4. Overall grazing intensity effect (no, low, high) to variation in the population growth rate (λ) from a life Table response experiments (LTRE) variance decomposition analysis. The error bars are bootstrapped 95% confidence intervals.

(mean \pm SD effect: $|0.003 \pm 0.001|$) and interaction (mean \pm SD effect: $|0.020 \pm 0.0280|$) between year and grazing intensity on λ . No grazing had a net positive effect on λ while both low and high grazing intensity had a negative effect (Fig. 4). In abandoned plots (no grazing), sexual reproduction (F; fecundity) was low causing a negative effect on the growth rate (Fig. 5). However, this negative effect was counterbalanced by a much larger positive effect of clonal reproduction (CR) which in sum caused the positive effect on population growth rates. In grazed plots (both low and high grazing intensity), the negative effect was caused by low clonal reproduction (CR). Plots under low grazing intensity also showed low sexual reproduction (F). Plots under high grazing intensity on the other hand, showed high sexual reproduction (F), but this was counterbalanced by an even lower clonal reproduction (CR). Among populations under no grazing intensity, the net effect on λ varied greatly while the net effect varied less among the grazed populations (Fig. S1 in the online version at DOI: [10.1016/j.flora.2016.04.007](https://doi.org/10.1016/j.flora.2016.04.007)). The positive contribution of clonal reproduction to λ was particularly clear in one of the populations under no grazing intensity (Fig. S2 in the online version at DOI: [10.1016/j.flora.2016.04.007](https://doi.org/10.1016/j.flora.2016.04.007)).

4. Discussion

In our study area *Knautia arvensis* ramets were grazed by cattle. Grazing reduced the number of inflorescences per ramet and the proportion of flowering ramets within the population. This could be due to the cattle's preference for *K. arvensis*. It is known that *K. arvensis* improves N efficiency for ruminants in vitro (Hoffmann et al., 2008), suggesting that it might be a preferred plant among cattle. Grazing also affected seedling establishment within populations, which was lowest in populations within abandoned grasslands. This is not surprising as the absence of small-scale disturbances (e.g. trampling) causes few gaps only in which seedlings can establish (Eriksson and Ehrlén, 1992). Low seedling establish-

Table 2
Estimated fixed effects statistics for linear mixed models with responses: survival to the next year ($t+1$) (survivals), proportion of seedlings (seedlings), proportion of flowering ramets (flowering ramets), number of inflorescences per flowering ramet (inflorescences), proportion of clonal reproduction (clonal reproduction), and proportion of grazed ramets (grazed ramets). The explanatory variables studied were: year (2008, 2009, 2010), grazing intensity (no, low, high) and interactions between years and grazing intensities. Models were fitted with backward selection and bold test statistics indicate $p < 0.05$.

Explanatory variable	Survivals ^a		Seedlings		Flowering ramets		Inflorescences		Clonal reproduction ^b		Grazed ramets ^c	
	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z	Estimate	z
Intercept	1.819	8.303	-6.387	-5.559	-0.605	-1.480	-0.129	0.142	1.396	-6.588	0.262	0.419
Year 2009	-0.718	-4.956	1.685	1.395	-0.453	-2.730	0.064	1.502			-1.087	-5.896
Year 2010			1.768	1.488	-0.043	-0.265	-0.078	-1.815	0.761	4.146	-0.932	-5.221
Grazing low			-12.769	-0.013	0.507	0.710	-0.618	-4.632	0.358	0.923	-1.461	-1.420
Grazing high			4.376	3.648	-2.693	-4.036	-0.864	-3.497	-0.127	-0.398		
Year 2009: Grazing low			11.742	0.012	-1.090	-3.608	0.215	3.444			2.344	5.672
Year 2009: Grazing high			-4.457	-3.415	0.293	0.874	0.167	1.096				
Year 2010: Grazing low			12.377	-1.919	-1.073	-3.679	0.270	4.420	-0.754	-2.183	1.184	3.061
Year 2010: Grazing high			-2.365	-1.919	0.338	1.080	-0.355	-1.937	-1.204	-4.357		

^a Year 2010 not included in the model.

^b Year 2008 not included in the model.

^c No grazing not included in the model.

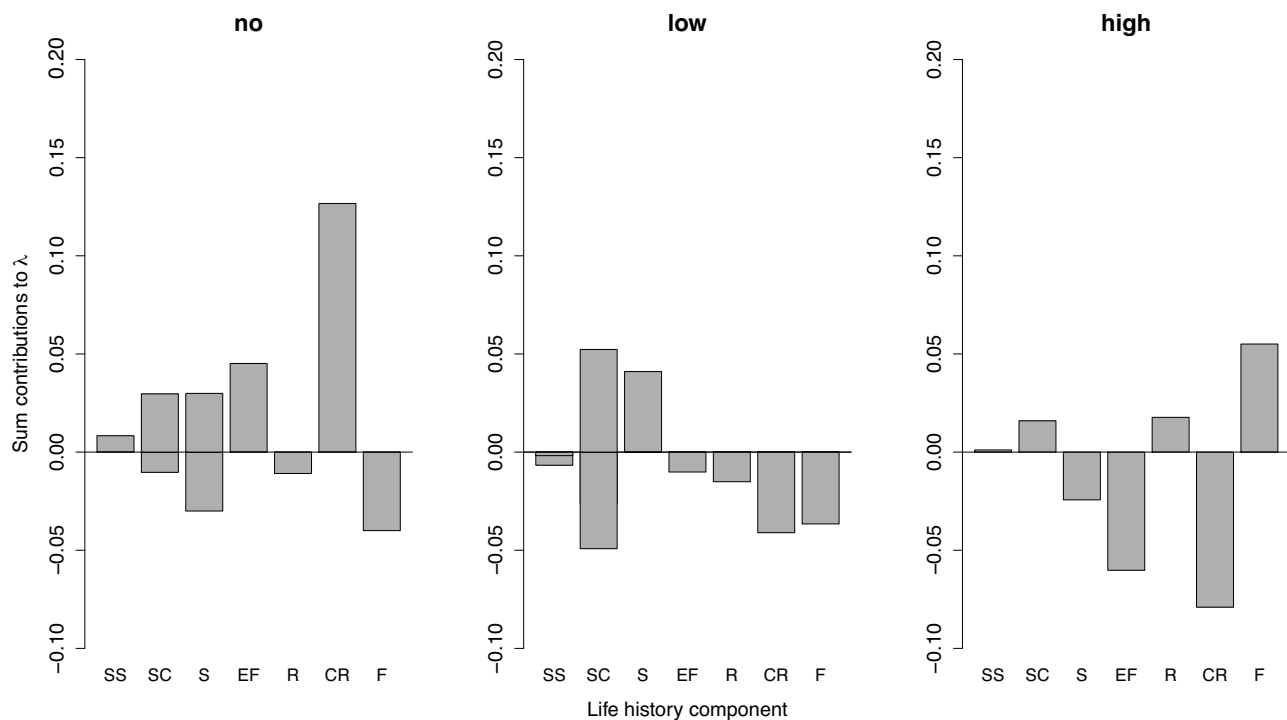


Fig. 5. Grazing intensity effect (no, low, high) to variation in the population growth rate (λ) from a life Table response experiments (LTRE) variance decomposition analysis. Transitions in the matrix are grouped according to life-history components: seedling survival (SS), survival of clonal offspring (SC), stasis (S), entering flowering stage (EF), retrogression (R), clonal reproduction (CR) and fecundity (F). Retrogression is defined as the transition from flowering to non-flowering stage.

ment in abandoned grasslands has been reported in several studies (Hamre et al., 2010; Poschod et al., 2011).

The effect of management was much larger than the year effects on the projected population growth rate. However, the clonal transition rates in 2008–2009 were estimated from $t+1$, and hence there was no variation in these transitions between years. Both the variation in clonal transitions between years and the year effect in the LTRE analysis are therefore likely to be underestimated.

Even though grazing reduced the proportion of flowering ramets and number of inflorescences per ramet and increased seedling establishment, this did not affect population growth rates significantly. A lack of effect of management on the growth rate can indicate that *K. arvensis* is not dependent on managed semi-natural grasslands to persist. However, a habitat modelling study shows that even though *K. arvensis* occurs in several vegetation types in Norway, semi-natural grasslands are by far its most common habi-

tat (Hovstad and Grenne, 2012). The large impact on the overall growth rates by survival of non-flowering rosettes indicates that the longevity of ramets is important for population survival. Herbaceous plants with long life-spans are known to have more stable populations because for such species survival is less variable than fecundity (Garcia et al., 2008). Populations of long-lived organisms may be able to buffer negative effects on vital rates even in small population sizes (Kolb et al., 2010). Longevity can therefore buffer temporal fluctuations in the population size.

In the grazed grasslands in our study area, sexual reproduction contributed the most to the growth rate whereas in abandoned grasslands clonal reproduction contributed the most. Fecundity and clonal growth are known to be negatively correlated for clonal plant species (Silvertown et al., 1993). The proportion of seedlings was largest in populations under high grazing intensity, even though the proportion of flowering ramets was least. This means

that the few flowering ramets in the populations under high grazing intensity contribute significantly to the population growth rate; sexual reproduction contributes more to population growth rate in grazed grasslands compared to abandoned grasslands. Grime (2001) states that responses to disturbance often involve adaptive shifts in regenerative traits. *Knautia arvensis* is a species with multiple reproduction strategies, which is an advantage in variable environments (Grime, 2001). Several remnant populations resist extinction because parts of their life cycle (Eriksson, 1996) and life history stages other than flowering ramets maintain the population. Populations in abandoned semi-natural grasslands can be remnant populations that survive for decades and have high growth rates due to high survival and clonal reproduction (Endels et al., 2007b; Hamre et al., 2010; Johansson et al., 2011). The results in this study show that *K. arvensis* is able to persist even if its habitat changes, but the results also indicate that the species can form remnant populations with very low rates of sexual regeneration if semi-natural grasslands are left without management.

The three grasslands without present domestic grazers were all former hay meadows in which hay harvesting ended in the mid-1980s. The two grasslands with the lowest population growth rates were occasionally grazed, and then under very low stocking rates, by horses and sheep until about year 2000. The third grassland with the exceptionally high population growth rates was not grazed at all by domestic animals after abandonment. These differences in management history may explain the large differences in clonal reproduction among the grasslands without grazing in this study. Lindborg and Ehrlén (2002) studied the perennial herb *Primula farinosa* and found that after abandonment of grazing by domestic animals the populations experienced a period of positive growth rate. However, by comparing historical and present distributions they concluded that most populations in habitats where grazing had ceased, had gone extinct. The exceptionally high growth rate of *K. arvensis* in one of the populations in abandoned grasslands is likely to last only a short time. The increased population growth might therefore be followed by a final population decrease as for *P. farinosa* (Lindborg and Ehrlén, 2002). To preserve viable populations of plant species inhabiting species-rich grasslands, such as *K. arvensis*, the effects of different management regimes must be monitored and evaluated in order to guide management decisions. It is essential to understand the reproduction and survival process in order to estimate if there are delayed responses in population size.

5. Conclusions

Knautia arvensis populations tolerate both grazing and short-term abandonment in semi-natural grassland and there were no differences in growth rates between populations in grazed and abandoned grasslands. A long life-span and survival of the species can, however, buffer changing environmental conditions. In populations in grazed grasslands, fertility contributed more to the growth rate than in abandoned grasslands where clonal regeneration contributed the most, which indicates a trade-off between the life-history components.

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