Effects of abandonment on *Tofieldia calyculata* (Liliaceae), a common, subdominant wetland species

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Summary

1 Cessation of mowing threatens the species richness of calcareous fen meadows. Especially populations of small rosette species are endangered by abandonment and are likely to go extinct in the long term. While this effect has been repeatedly demonstrated for rosette species that reproduce only by seeds, it is not yet clear whether it also applies to small rosette species that are able to grow clonally, since clonality may permit survival if sexual reproduction is inhibited after abandonment. We investigated the impact of abandonment on *Tofieldia calyculata,* a common clonal prostrate species of calcareous fen meadows.

2 The population density of *T. calyculata* (ramets m^{-2}) was not significantly lower in fallows than in mown fens, even though it was negatively correlated with the biomass production, which tended to increase after abandonment. Morphological traits of *T. calyculata* (e.g. leaf number or size) did not differ consistently between fallows and mown fens.

3 Abandonment strongly affected the reproduction of *T. calyculata.* The proportion of plants producing daughter tillers increased from 67% to 91%, and the mean number of daughter tillers per mother tiller increased from 1.0 to 1.7. The proportion of flowering tillers and the germination rate of seeds decreased only slightly after abandonment, but seedling recruitment was virtually non-existent in abandoned fens.

4 In the short term, *T. calyculata* appears able to buffer the negative effects of abandonment, i.e. to maintain its population density through clonal growth. However, clonal growth seems to be enhanced at the expense of sexual reproduction. This might lead to a population decline in the long term, especially at more productive sites.

Keywords: calcareous fens, fallow, litter accumulation, reproduction, population dynamics, phenotypic response

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Introduction

Calcareous fen meadows are diverse ecosystems with high species richness and many rare plant species (Wheeler 1988; Landolt 1991). Nearly 50% of the threatened plant species of Switzerland occur in fens, yet roughly 90% of all Swiss wetlands have disappeared since 1850 (BUWAL 1990) and the remaining ones are threatened by land-use changes,

such as intensified farming or abandonment. Fen meadows depend on extensive agricultural use such as late-season mowing or livestock grazing.

Cessation of mowing leads to secondary succession, with the replacement of typical fen species by species from other vegetation types, especially tall herbs, shrubs and trees. The competitive ability of species in fallows mainly depends on their life form (Schiefer 1981) and architecture. Short-term abandonment may increase the vigour and seed production of dominant graminoids and facilitate seed set in late-blooming forbs (Diemer & Pfadenhauer 1987; Bosshard *et al.* 1988; Schopp-Guth *et al.* 1994; R. Billeter, pers. observ.), but small, short-lived perennials reproducing regularly by seeds are suppressed (Jensen 1997). Bosshard *et al.* (1988) found 29% more phytomass in abandoned fens than in mown ones, mainly because of litter accumulation. As a result, prostrate rosette species such as *Parnassia palustris* drastically declined in density. In an earlier study, Preiss (1982) observed a decrease in the density of *P. palustris* and *Polygala amarella* in fens 10–15 years after abandonment. This is in accordance with the finding of Pfadenhauer & Maas (1987) that the population density of *P. palustris* is highest in regularly mown fen meadows. The presence of litter in fallows also inhibits the germination and seedling establishment of small rosette species (Bosshard *et al.* 1988; Jensen 1997). Thus, populations of prostrate rosette species which depend on sexual reproduction are likely to become extinct during secondary succession.

However, it is unclear to what extent these results also apply to prostrate species that are able to grow clonally. These species might be able to buffer the negative effects of abandonment at least in the short term *via* enhanced clonal growth. Recent modelling has shown that vegetative reproduction is favoured in perennials if survival rates of older life stages are high (Takenori & Hisao 1996). As abandonment is expected to enhance the survival of established plants, *T. calyculata* might increase its resource allocation to clonal growth in fallows. Furthermore, Hegazy (1994) showed that in *Heliotropium curassavicum* sexual reproduction was favoured in open habitats, whereas clonal growth was more frequent at closed, overgrown sites. Abandonment might have a similar effect on reproduction, as litter accumulates and biomass production increases, so that canopies become denser after the cessation of mowing.

The aim of this study is to investigate the impact of abandonment on a small, prostrate species, *Tofieldia calyculata,* which is able to produce clonal offspring. The main questions are: (1) Does continued abandonment lead to a population decline of *T. calyculata?* (2) Do plant traits vary in response to management status? (3) Do litter and above-ground biomass influence these traits? (4) Does *T. calyculata* increase its allocation to clonal growth in the course of succession, i.e. can we find a trade-off between clonal growth and sexual reproduction? To separate short-term and long-term effects, we examined the population structure of *T. calyculata* along a chronosequence of abandonment.

Materials and methods

STUDY SPECIES

Tofieldia calyculata (L.) WAHLENB. (Liliaceae) is a subdominant, but common species of fen meadows. It is a small, prostrate herb flowering in May or June. The leaves of the rosette form an appressed fan with the flowering stalk arising in its centre. The inflorescence is 15–20 cm long with light yellow flowers and generally produces more than 500

seeds. However, the species can also grow clonally by forming daughter tillers. A tiller can remain vegetative for at least two years, but it dies after flowering (R. Billeter, pers. observ.). Plants can form large clones consisting of up to 20 fans; of these, only one or two ramets flower simultaneously.

FIELD SITES

The focus of this study are montane fens (altitude >800 m a.s.l.) in NE-Switzerland (cantons St. Gallen, Schwyz, Appenzell). The climate is rather cool and humid with a mean annual daytime temperature of 7–8 °C and an annual precipitation of 1700–1900 mm (mean 1988–1997).

In each of seven regions we selected one to three abandoned fens as well as one fen mown annually as control, i.e. in total 16 fallows and seven mown fens, all belonging to the phytosociological alliance Caricion davallianae (Ellenberg 1996). Fallows varied in age since abandonment (4–35 yrs). Within each fen, we randomly placed four permanent plots (2 m x 1 m) in May or June 1998. To assure that *T. calyculata* was present in all plots, plots without the species were rejected and replaced by randomly selected new plots.

The biomass and litter production of each fen were determined by sampling at peak plant biomass in August 1998. Along the edges of each plot, we cut the vegetation at ground level in two squares of 18.5 cm x 18.5 cm. Samples were separated into biomass and litter, dried at 80 °C for 24 h, and weighed.

MEASUREMENTS ON *T. CALYCULATA*

To assess the population size of *T. calyculata,* we placed parallel transects across the fen in 1999. Along these transects we randomly selected twenty 1-m^2 squares and counted all inflorescences of *T. calyculata* within the squares. The average number of inflorescences per squaremetre was divided by the average proportion of flowering tillers to obtain an estimate of population density, expressed as the total number of tillers per m^2. Population size was estimated by multiplying population density with the area of the fen.

To study growth and fecundity, three plants of *T. calyculata* were randomly chosen within each permanent plot in June 1998 and marked with coloured wire and tags. The plants were surveyed twice, in August 1998 and 1999. Seven of the 23 fens could not be surveyed any more in 1999 due to accidental mowing of fallows by farmers. We measured the following traits: number of leaves in the fan, length of the largest leaf in the fan, number of daughter tillers (if present), and length of the flowering stalk as well as of the inflorescence (if present). The proportion of shoots with daughter tillers and the proportion of flowering shoots were determined, and their ratio was calculated as a measure of the relative importance of clonal growth and sexual reproduction.

To estimate recruitment and seedling establishment in the field, we randomly selected five 10 cm x 10 cm squares within each plot and counted all seedlings of *T. calyculata.* Seedlings were marked in June 1999, and their survival was checked after 1.5 months in late July/August 1999.

To determine germination rates of seeds, the inflorescences of all marked *T. calyculata* were collected in summer 1998. If a marked plant did not flower, we randomly collected an inflorescence nearby. In addition, we collected three more inflorescences from around the plots. The inflorescences were pooled per site and 500 seeds were haphazardly chosen for the germination experiment. Seeds were first stratified at –4 °C for four weeks. Afterwards five groups of 100 seeds each were

placed in Petri dishes containing vermiculite. These dishes were placed in a climate chamber, using a day/night regime of 14/10 h, 20/10 °C. We followed germination for three months. After germination we transplanted the seedlings into a mixture of sand and mineral soil and kept them in the greenhouse for a survey of establishment.

DATA ANALYSIS

Differences in abundance, growth and reproductive traits were tested with hierarchical multiple regression analysis. The effect of region, management status (fallow *vs.* control) and age of fallow were tested against the variation among individual sites. Region, management status and site were factors, while age was a continuous variable nested within management status.

The analysis was also repeated with either total above-ground biomass or litter mass as a covariable. For population size and density we also included the size of the fen in the model. Population size, population density, length of flowering stalk and litter mass were log-transformed to obtain normally distributed residuals. The remainder of the variables were analysed without transformation. All analyses were done with Genstat 5.0 (Payne *et al.* 1995).

Results

POPULATION SIZE AND GROWTH

The population size of *T. calyculata* did not decrease significantly after abandonment (management status: $P > 0.1$, Table 1); it mostly depended on the size of the fen ($P < 0.01$) and differed among regions ($P < 0.05$). The density of tillers of *T. calyculata* was unaffected by abandonment ($P > 0.1$, Table 1) and independent of the size of the fen or region.

Only few effects of abandonment on the growth of *T. calyculata* could be observed. The length of the longest leaf in the marked fans increased significantly after abandonment in 1998 (fallow, 11.8 ± 0.3 cm; control, 8.7 ± 0.3 cm, mean ± *SE*, $P < 0.01$; Table 2). In addition, the number of leaves per fan was significantly higher in fallows (11 ± 0.3) than in mown controls (7 ± 0.5, $P < 0.05$) in 1998. However, in 1999, neither management status nor age since abandonment had an effect on the longest leaf or the number of leaves (Table 2). The length of the flowering stalk as well as the length of the inflorescence did not change in response to management status or age of abandonment in either year.

CLONAL GROWTH AND SEXUAL REPRODUCTION

Clonal growth was clearly enhanced by abandonment. In 1998, the proportion of plants producing daughter tillers and the number of daughter tillers per plant significantly increased with fallow age (Table 1, 2). In 1999, the mean number of daughter tillers per plant was significantly higher in fallows (1.7 ± 0.2) than in controls (1.0 ± 0.1, $P < 0.05$, Table 2), and likewise the proportion of plants producing daughter tillers was much higher in fallows (91 ± 2.5%) than in controls (67 ± 7%, $P < 0.001$).

The proportion of flowering plants was independent of management status in 1998 ($P > 0.1$), but in 1999, a slightly lower proportion of plants flowered in fallows ($P < 0.1$, Table 1). The trade-off ratio increased linearly with age since abandonment in 1998 ($P < 0.001$, Table 1) and was higher in abandoned than in mown fens in 1999 ($P < 0.05$, Table 1). In 1998, the ratio was significantly different between the regions ($P < 0.01$).

Only very few seedlings of *T. calyculata* were found in the control plots, and none in the fallows. Hence, we could not perform a statistical analysis. However, this result indi-

Table 1. *ANOVA table for the effects of abandonment and region on the abundance and reproduction of* Tofieldia calyculata, *based on hierarchical multiple regression. (*),* $P < 0.1$; **,* $P < 0.05$; ***,* $P < 0.01$; ****,* $P < 0.001$; *no symbol,* $P \geq 0.1$

	Population size 1999		Population density 1999		Proportion of clonality				Proportion flowering				Trade-off ratio			
					1998		1999		1998		1999		1998		1999	
Source of variation	df	*MS*	df	*MS*	df	*MS*	df	*MS*	df	*MS*	df	*MS*	df	*MS*	df	*MS*
Size of the fen	1	19.2 **	1	0.29												
Region	5	5.2 *	5	2.28	6	0.03	5	0.02 *	6	0.12 *	5	0.03	6	0.06 **	5	0.06
Fallow *vs.* mown	1	2.2	1	0.95	1	0.02	1	0.26 ***	1	0.04	1	0.17 (*)	1	0.0003	1	0.65 *
Fallow age	1	0.43	1	0.04	1	0.13 *	1	0.001	1	0.09 (*)	1	0.02	1	0.15 ***	1	0.04
Residual (site)	11	1.4	11	1.88	15	0.03	9	0.006	15	0.02	9	0.04	15	0.01	9	0.09

Table 2. *Significance of the effects of abandonment and region on phenotypic traits of* Tofieldia calyculata, *obtained from hierarchical multiple regression. (*),* $P < 0.1$; **,* $P < 0.05$; ***,* $P < 0.01$; ****,* $P < 0.001$; *ns,* $P \geq 0.1$

	Length of longest leaf		Number of leaves		Length of inflorescence		Length of flowering stalk		Number of daughter ramets		Germination rate
Source of variation	1998	1999	1998	1999	1998	1999	1998	1999	1998	1999	1998
Region	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Fallow *vs.* mown	**	ns	*	ns	ns	ns	ns	ns	ns	*	ns
Fallow age	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	(*)

cates that sexual reproduction of *T. calyculata* is very scarce in the study sites, and possibly completely inhibited in the fallows. Germination of seeds in the climate chamber was rather poor, with germination rates ranging from 0.0% to 8.2% with a mean of 3.3% in controls and 2.2% in fallows ($P > 0.1$). Overall, germination rate tended to decrease with the age of the fallow ($P < 0.1$, Table 2). None of the seedlings became established after being transplanted and kept under controlled conditions. All of them died within a few days.

EFFECTS OF LITTER AND ABOVE-GROUND BIOMASS

Litter mass increased significantly after abandonment ($P < 0.001$). Therefore, when litter mass was introduced as a covariable in data analysis, the effect of management status was no longer significant. Litter mass especially affected reproductive traits such as clonal growth, frequency of flowering and trade-off ratio (see Fig. 1).

Above-ground biomass was highly correlated with litter mass ($P < 0.001$) and tended to increase after abandonment ($P < 0.1$). Nevertheless, adding above-ground biomass as a covariable in our analysis did generally not influence the results obtained for management status. Only the population size and density of *T. calyculata* were negatively correlated with biomass ($P < 0.001$ for size; $P < 0.01$ for density, Fig. 2).

Discussion

NO EFFECT OF ABANDONMENT ON POPULATION SIZE AND GROWTH?

Tofieldia calyculata did apparently not suffer severely from the effects of abandonment, as populations did not clearly decline in size after the cessation of mowing (see Table 1). This is opposite to the findings of Preiss (1982), Bosshard *et al.* (1988) and Jensen (1997), who observed a decline of prostrate rosette species in fallows. Possible reasons for a decline would be (a) the accumulation of litter, which

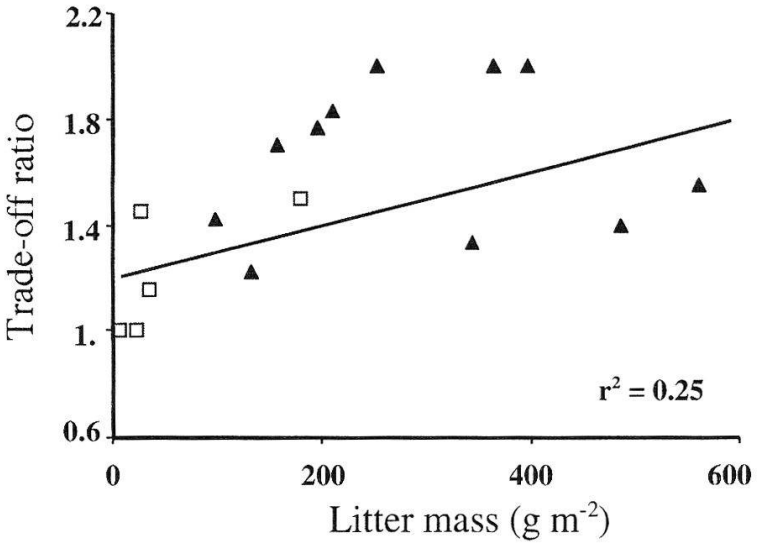

Fig. 1. *Linear regression fit for the trade-off ratio (proportion of shoots with daughter tillers / proportion of flowering shoots) of* Tofieldia calyculata *in 1999 against litter mass. Each symbol represents one population (▲, fallows; □, mown controls).*

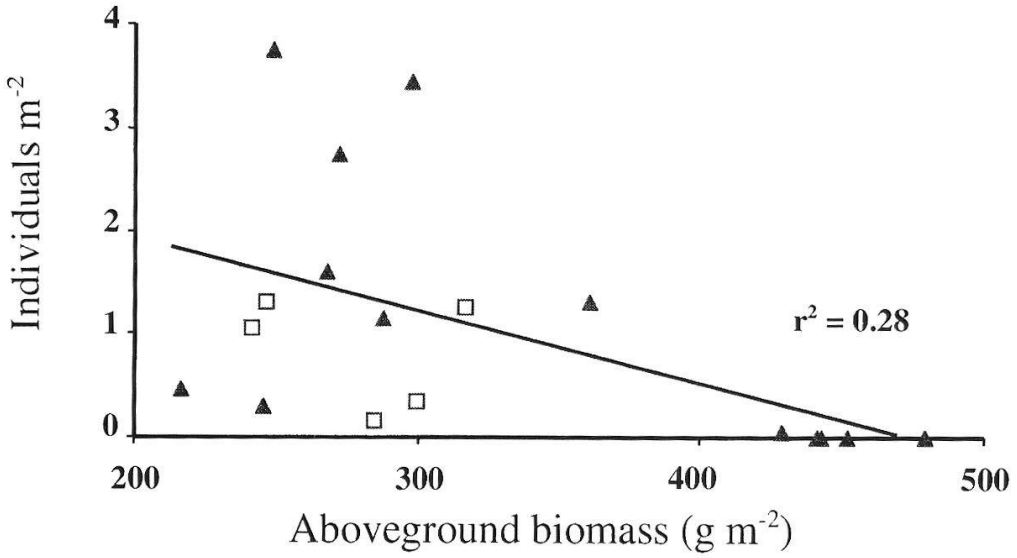

Fig. 2 Linear regression fit for the population density (number of individuals m^{-2}) of Tofieldia calyculata *in 1999 against the above-ground biomass of the vegetation. Each symbol represents one population (▲, fallows; □, mown controls).*

constrains recruitment and establishment of seedlings (Bosshard *et al.* 1988; Maas 1988, Oostermeijer *et al.* 1994; Jensen & Schrautzer 1999), and (b) auteutrophication, i.e. the accumulation of nutrients, which increases the productivity of the fen (Léon 1968; Preiss 1982; Stöcklin & Gisi 1989a, b; Thorn 2000). The fact that above-ground biomass tended to be higher in the fallows and its positive correlation with litter mass support the idea that auteutrophication occurred after abandonment. The negative correlation between above-ground biomass and population density (see Fig. 2) shows that the fate of *T. calyculata* was correlated with the productivity of the fen, probably because plants were shaded out in the dense vegetation of more productive sites. Therefore, abandonment particularly threatens the persistence of *T. calyculata* if it is associated with higher productivity.

That phenotypic traits did not change consistently after abandonment, was surprising (Table 2). The results of 1998 suggest that *T. calyculata* responded to shading in fallows. The higher number of leaves as well as their greater length might have enhanced the photosynthetic yield of *T. calyculata*. However, the data from 1999 did not confirm this result since there was only a very weak trend towards longer leaves, and the number of leaves was unaffected. Furthermore, all other growth traits did not respond to management status in either year. This suggests that *T. calyculata* is not very plastic in its response at the tiller level. Most of its plasticity emerges at the genet level in the production of daughters and inflorescences.

A possible reason for the difference between the results obtained in 1998 and in 1999 is that climatic conditions differed. The comparison of the annual means of 1999 and 1998 with the long-term records of the Swiss meteorological institute indicates that weather conditions in 1998 were quite similar to the previous decade, whereas 1999 was cooler (–0.6 °C) and wetter (+420 mm precipitation), and with more snow in January–May (+59.5 cm). Therefore, the growing season

started at least a month later in 1999 than in 1998. At the time of our field survey in August, the phenology of the vegetation was still a month behind compared to 1998, and we may have missed the maximal growth of the 1999 season. Hence differences may not yet have been pronounced enough to be statistically significant.

CLEAR EFFECT OF ABANDONMENT ON REPRODUCTION

An increase in the proportion of individuals with daughter tillers, as well as in the number of daughter tillers per mother fan after abandonment was obvious in both years, but more pronounced in 1999 (Tables 1 and 2). For the proportion of flowering plants a decrease following abandonment was less obvious but still apparent (Table 1). More importantly, the germination experiment suggested that the germination rate of seeds declines progressively after abandonment (Table 2). In addition, the overall germination success seems to be generally low in *T. calyculata,* and the establishment of seedlings in the field is extremely rare. *Tofieldia calyculata* is a species with very small seeds and such species are especially limited in germination and establishment by the formation of a litter layer (Carson & Peterson 1990; Tilman 1993; Jensen 1997; Foster & Gross 1997). Therefore, the establishment of new *T. calyculata* seedlings is highly unlikely, and indeed, we could not find any established seedlings of *T. calyculata* in fallows.

The trade-off ratio, calculated as the ratio between the proportion of plants with daughter tillers and the proportion of flowering plants, was significantly related to abandonment in both years. In 1998, the investment in clonal growth increased with the age of the fallow (Table 1). These results are consistent with the findings of Hegazy (1996), who observed an increase in clonal reproduction in closed, overgrown sites, and with the modelling of Takenori & Hisao (1996), who showed that high survival rates of adult plants (which we expect in fallows) favour clonal growth compared to sexual reproduction. Stöcklin (1999) found that an allopatric (sub-)species of *Epilobium* persisting in a more stressful environment grows clonally while others do not. However, the data of Stöcklin (1999) suggest that clonal growth is not necessarily associated with reduced reproduction by seeds. This is in accordance with our finding that clonal growth in *T. calyculata* increased after abandonment, while flowering only slightly decreased (Table 1). As an explanation for this pattern, Stöcklin (1999) proposed that long-term survival of established populations may depend largely on clonal spread, but the colonisation of new sites requires recruitment from seeds. Similarly, Schmid (1990) concluded in his theoretical paper that sexual reproduction is necessary for the establishment of new populations, but not for the persistence of the established ones. Thus, from an evolutionary point of view it seems that a species should maintain its seed production even when it allocates more resources to clonal growth. However, resources are limited. The low germination rate of seeds and the low survival of seedlings in our fallows might be due to reduced resource allocation to individual seeds. Possibly, the trade-off constraining *T. calyculata* is not between the production of daughter tillers and the production of seeds, but between the production of daughter tillers and seed viability.

CONCLUSIONS

Small clonal rosette species, such as *T. calyculata* may have the same fate in fallows as non-clonal species, e.g. *Parnassia palustris,* although clonal growth can buffer against

population extinction in the short term. However, the costs of this increased clonal growth are slightly reduced flowering and clearly reduced viability of seeds and seedlings. Consequently, a decline of populations after abandonment seems to be inevitable in the long term, especially in more productive fallows. On the other hand, the high persistence of single plants in old fallows gives hope for the restoration of abandoned fens. These individuals can possibly act as sources for population expansion in previously unmanaged fallows, after management has been resumed.

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