

## Ramet performance in two tussock plants — Do the tussock-level parameters matter?

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### Abstract

Studies in plant demography are primarily done at the level of ramets and typically collect ramet-related parameters such as ramet size, type and history. This approach ignores possible effects of factors associated with higher levels, such as genet or tussock. This is particularly important in perennial resprouting herbs with persistent root that consists of many ramets as interaction between ramets, both by competition and by resource sharing, are likely to be intense in these plants. This study investigates effects of tussock-level parameters (age, size and ramet position within tussock and ramet density) on performance of individual ramets in two tussock-forming resprouting herbs (*Tanacetum vulgare* and *Centaurea jacea*).

The results show that position of a ramet within tussock did not affect ramet growth, but had significant effects on flowering and survival in both species. The direction of the effect differed between the two species; marginal ramets were more successful in *T. vulgare*, while central ramets were more successful in *C. jacea*. In addition, tussock age had a significant effect on ramet flowering and survival in *T. vulgare*. Both these effects are likely to be due to the more competitive life form of *T. vulgare*, which is restricted to temporary habitats with intense competition. *C. jacea* is a species of mown or grazed grasslands with lower productivity, which are more stable and where competition is weaker. The effects of the number of neighboring ramets and of the tussock size were significant, but often locality-specific.

The results indicate that although many important effects of tussock-related parameters exist, their direction and magnitude differ between species or even populations and are thus not easily predictable. Neglecting these effects, however, is likely to make the demographic models weaker.

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**Keywords:** Tussock age; Position within tussock; Tussock size; Number of neighbors; *Tanacetum vulgare*; *Centaurea jacea*; Clonal plants

### Introduction

Large majority of all plants are hierarchically organized; in most perennial plants, individual ramets are parts of larger units, such as tussocks or clonal fragments connected by rhizomes or roots. Owing to

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this hierarchical organization, there is no necessary basic level at which demography is to be studied (Harper and White, 1974). While there are studies addressing demographical processes at different levels of hierarchy of plant bodies simultaneously (see Damman and Cain, 1998; De Kroon et al., 1992; Hartnett and Bazzaz, 1985), they are not very common. For practical reasons, most studies of plant demography restrict themselves to the level of ramets (Bishop et al., 1978; Cook, 1985; Hossaert-McKey and Jarry, 1992) and work only with characteristics that can be defined without a reference to larger units to which the ramet belongs (Carlsson and Callaghan, 1990, 1991; Eriksson, 1988; Thompson and Beattie, 1981).

Such an approach is acceptable only when the behavior of individual ramets is essentially independent of the position of the ramet within the tussock/clonal fragment, or of the size or age of the whole tussock. If this is not the case, a loss of information on the system is likely when the dynamics of the system are studied only using ramet-level demographic parameters. Surprisingly, there is not much information available on the effect of tussock-level parameters on ramet behavior. The few existing examples on variation in ramet behavior due to ramet position within genet reported for clonal plants (Charpentier and Stuefer, 1999), tussock grass species (Briske and Butler, 1989) and in trees and shrubs (Acosta et al., 1993; Suzuki, 2000) make the assumption of identical behavior of ramets difficult to maintain (Armstrong, 1982, 1983).

This problem is particularly important for perennial resprouting tussock-forming plants. In these plants, tussocks are quite well defined and often remain integrated over the life span of the species. Their ramets are clumped and often they are placed all over the rhizome or the root. Owing to the physical proximity and physiological integration of ramets, they are likely to interact both by competition and by resource sharing. Therefore their behavior may thus reflect both tussock-level parameters such as tussock age or size (i.e. ramets may differ in their performance depending on the size or age of the tussock), and position of the ramet within the tussock (i.e. ramets may differ in their performance depending whether their position is marginal or central). While there are generally very few hard data on the effects of genet-level parameters on ramet performance, in tussock-forming herbs such studies are completely lacking (Crawley, 1997). This study therefore aims to study effects of tussock-level parameters on performance of individual ramets of tussock-forming resprouting herbs.

We selected two perennial tussock-forming species, *Tanacetum vulgare* L. and *Centaurea jacea* subsp. *jacea* L. Both these species are tussock forming resprouting perennial herbs with clearly distinct annual ramets connected by a persistent woody root. In both species

we asked how within-season performance of their ramets depends on tussock-related parameters, viz. (i) the size and age of the tussock and (ii) position of the ramet in the tussock. In order to do so, we removed the effect of usual ramet-level parameters, such as ramet initial size or neighborhood density, by regression techniques. The two species used here are very different in life history traits as well as in their habitat requirements. Agreement in conclusions between these two would therefore indicate that the patterns are robust over species and may have general validity. To strengthen the generality of the findings further, we also performed the study at more than one locality (at two different localities for *T. vulgare* and at three different localities for *C. jacea*). Again, agreement in the conclusions between the two localities would indicate general validity for the species, while differences would indicate that local environmental conditions determine the relationship.

## Methods

### Study species

To study the effects of tussock parameters on ramet performance we used two different species, *T. vulgare* L. and *C. jacea* subsp. *jacea* L. (*Asteraceae*). Tussocks of both species consist of many ramets connected by a common woody root. *T. vulgare* is a species of ruderal habitats, where it is often the dominant. The tussocks can reach up to 0.5 m in diameter and ramets may be up to 1.6 m in height (pers. obs.). In contrast, *C. jacea* is a species of perennial mown meadows. Its habitats are much more persistent than those of *T. vulgare* and competition for light is likely to be weaker there.

### Field data collection: *T. vulgare*

*T. vulgare* was studied in two localities: Klec (49°5'38.4"N, 14°45'14"E), a locality on a productive old-field, and Hromada (N 49°5'29.9"N, 14°45'50.3"E), a locality at debris deposits with very shallow soil. The two sites were selected based on our survey of the region to represent two extremely contrasting examples of all possible *T. vulgare* localities. Detailed description of the localities is given in Table 1. All localities are situated in the vicinity of Lužnice village, 6 km NE of town Třeboň, in south Bohemia, Czech Republic.

At each locality 50 tussocks were randomly selected for *T. vulgare*, by selecting the tussock closest to a random point on the area of 30 × 15 m at Klec and of 15 × 10 m at Hromada. The different plot size used at the two localities was due to differences in tussock densities. If no tussock was found within 0.5 m distance

**Table 1.** Main characteristics of the single localities used in the study

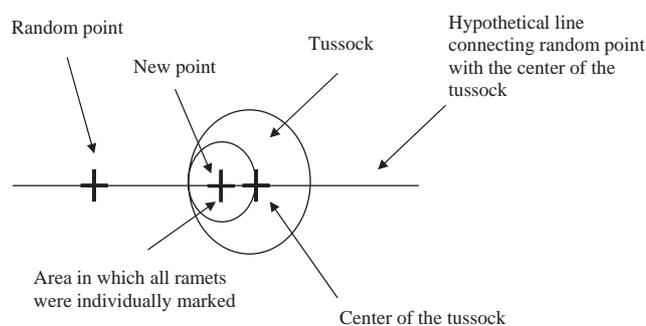
Species	Locality	Plant age	Tussock size	Tussock height	Description
<i>Tanacetum vulgare</i>	Klec	3.8 ± 0.2	11.3 ± 0.7	62.1 ± 1.3	Nutrient rich abandoned field, <i>Tanacetum vulgare</i> is the dominant species, single <i>Tanacetum vulgare</i> tussocks are at least 0.5 m apart, surrounded by smaller ruderal forbs, total cover of aboveground vegetation is approx. 70%
	Hromada	3.1 ± 0.1	5.4 ± 0.5	31.8 ± 1.4	Debris deposit with very shallow soil, nutrient poor and dry, <i>Tanacetum vulgare</i> is the dominant species, single <i>Tanacetum vulgare</i> tussocks are about 0.3 m apart, surrounded by other ruderal forbs, total cover of aboveground vegetation is approx. 40%
<i>Centaurea jacea</i>	Trojúhelník	3.1 ± 0.2	5.2 ± 0.6	19.1 ± 1.2	Shallow soil ruderal grassland, <i>Centaurea jacea</i> is rare at the locality, tussocks are at least 0.5 m apart, mown at least once a year, total cover of aboveground vegetation is approx. 90%
	Potěšil	4.3 ± 0.3	32.8 ± 1.9	31.4 ± 1.0	Shaded grassy dam of a pond, nutrient rich, <i>Centaurea jacea</i> is rare at the locality, tussocks are at least 0.5 m apart, not managed, total cover of aboveground vegetation is approx. 100%
	Lužnice	3.8 ± 0.3	27.3 ± 1.7	20.9 ± 0.6	Sandy road verge dominated by <i>Centaurea jacea</i> , tussocks are usually not more than 0.2 m apart, surrounded by low grassy vegetation, mown once every few years, total cover of aboveground vegetation is approx. 90%

Differences in plant age determine stability of the localities. Tussock size and height are determinants of site productivity. Values are means ± standard error of the mean.

(the typical distance between two neighboring tussocks) the point was discarded and a new point drawn. The 0.5 m limit was used to ensure that tussocks in low-density areas would not be over represented.

A hypothetical line connecting the random point with the center of the selected tussock was constructed and a new point was placed on this line 5 cm from edge of this tussock in the direction to its center. All ramets within 5 cm round this new point were individually marked with plastic rings and used for the study. Considering the typical diameter of a tussock (approximately 20 cm) this procedure enabled us to select ramets covering all possible positions within the tussock. See Fig. 1 for illustration of the selection process.

The ramets were selected and marked in the spring (May 23–27, 2001). At that time also the following parameters were measured: ramet height, stem diameter 2 cm above ground and number of living leaves longer



**Fig. 1.** Illustration of the way of selecting ramets of *Tanacetum vulgare* to be marked for the study. The approach combined random selection of tussocks with the aim to cover all possible ramet positions within the tussock. See text for details.

than 1 cm. In autumn (September 17–21, 2001) survival and flowering of each ramet was recorded and its size was measured using the same parameters as in spring.

Also the number of neighbors within 5 cm was counted. Relative position of each ramet within the tussock was estimated by placing a hypothetical line going through the target ramet and center of the tussock, and measuring the distance between the target ramet and both edges of the tussock lying at this line. Thereafter the ratio of distance to the closer edge and the sum of distances to the closer and further edge of the tussock were calculated. Then the ramet was harvested and divided into inflorescence (without peduncles) and the rest. The collected biomass was dried at 60 °C and weighted.

Number of flowering and non-flowering ramets were counted to estimate the size of the tussock. Plant age was estimated by counting the number of annual rings on the basal part of main root after dyeing by fluoroglucinol (Dietz and Ullmann, 1997, for the exact method of dyeing see Němec et al., 1962). To sample the root, the plants had to be dug out. Digging out the plants also enabled us to ensure that the ramets in the tussocks were really connected. Due to ramet mortality only 30 living tussocks per locality and 48 and 60 living ramets at Hromada and Klec, respectively remained for the analysis of ramet growth.

### Field data collection: *C. jacea*

*C. jacea* was studied at three localities: Trojúhelník (49°5'51.2"N, 14°45'47.7"E), a locality in the center of crossroads on shallow soil, Potěšil (49°5'29.8"N, 14°48'1"E), a locality on dam of a pond and Lužnice (49°4'3.1"N, 14°45'43.9"E), a locality on a field road verge. All tussocks at Potěšil (20 tussocks) and Trojúhelník (22 tussocks) localities were used. At Lužnice locality all tussocks within a 5 × 3 m square placed in the center of the locality were used (26 tussocks). The three sites were selected based on our survey of the region to represent three contrasting examples of all possible *C. jacea* localities. Detailed description of the localities is in Table 1. All the localities are situated in the same area as those used for *T. vulgare*.

Due to a different nature of the species, a slightly different recording procedure was used for *C. jacea*. Four ramets were marked per tussock, two at opposite edges of the longest diameter of the tussock, one in the center and one closest to the one in the center.

In spring the following parameters were measured: ramet height, ramet diameter above ground and number of living leaves longer than 1 cm. In autumn, the same parameters as in spring were measured, except of counting the number of inflorescences instead of leaves in flowering ramets. Survival and flowering of each ramet was recorded and the number of neighbors within 2.5 cm and distance to the closest ramet were estimated.

Position of ramets within the tussock and size and age of the tussock were estimated using the same method as for *T. vulgare*.

### Data analysis

Regression analysis was used to explore interdependence of the tussock level variables. Since plotting of the data showed that all the relationships are linear, linear regression only was used to estimate the relationship between number of neighbors and position within tussock and number of neighbors and tussock size.

We used analysis of covariance to study importance of ramet and tussock level parameters on ramet growth. Ramet diameter and height in autumn and number of inflorescence per ramet were used as dependent variables for *C. jacea* and autumn biomass and inflorescence biomass per ramet for *T. vulgare*. The independent variables were divided into two groups: variables defined at the level of tussock and defined at ramet level. Independent variables defined at the level of tussock were locality, number of fertile ramets, number of sterile ramets, and tussock age; independent variables defined at the level of ramet were spring ramet height and diameter, number of leaves in spring, number of neighboring ramets (within 5 cm for *T. vulgare* and 2.5 cm for *C. jacea*), relative position within the tussock and distance to the closest neighboring ramet (only for *C. jacea*). Testing variables from these two groups was then based on different error levels. Using the two error levels enabled us to take into account the fact that ramets within the same tussock are not independent. Thus the error degrees of freedom for ramet-level parameters reflect number of ramets, while it reflects number of tussocks for the tussock-level parameters. Spring sizes were used as covariates in all the tests.

Survival and flowering probabilities of ramets were tested using logistic regression with the same independent variables as above; for test of parameters at the level of ramets tussock code was used as a factor. In all tests a hierarchical type SS I model was used. This provided us with a test of the net effect of each parameter after adjusting for the effect of all preceding parameters in the model. All tests were performed using S-Plus 6 for Windows (2001).

### Results

Examination of all the tussocks at the end of the experiment confirmed that all the ramets considered as belonging to one tussock were really physically connected. Therefore the relationships recorded at the within tussock level may be interpreted either as due to intra-clonal regulation or as due to competition. The

distance between two neighboring ramets was never more than 5 cm, while the minimum distance between neighboring tussocks was 20 cm. Therefore we can expect that within a tussock ramet only will experience intra-tussock interactions, whereas peripheral ramets will also experience inter-specific interactions. Inter-tussock interactions are, given the distance between the tussocks, not expected to be important.

### Effects of local density and tussock size

Summaries of the tests of effects of all parameters on ramet growth, flowering and survival are given in Table 2 for *T. vulgare* and in Table 3 for *C. jacea*. Number of neighboring ramets did not have any effect on autumn biomass and survival in *T. vulgare* at Klec. However it had a significant positive effect on autumn biomass and a significant negative effect on survival of *T. vulgare* at Hromada (Figs. 2 and 3). In *C. jacea*, survival of ramets was negatively affected by number of neighbors at Trojúhelník and positively at Potěšil, whereas no effect was found at Lužnice. It had neither an effect on ramet growth in *C. jacea*, nor on flowering in both species.

Size of the tussock (number of fertile and sterile ramets) enhanced ramet growth at Hromada for *T. vulgare*, but it had no effect at Klec. The proportion of sterile ramets in a tussock negatively correlated with ramet survival at Hromada. In *C. jacea*, ramet growth was positively correlated with proportion of flowering ramets at all localities. Size of the tussock did not have any effect on flowering in both species neither on survival in *C. jacea*.

### Effects of other tussock-related parameters

Position within tussock did not affect ramet growth in any of the species. Ramets in the center of the tussock however invested less in flowering and had lower survival rates in *T. vulgare* at both localities. In *C. jacea*, survival was lower at the edge of the tussock. Flowering was not affected by position within tussock in this species.

Tussock age had a significant negative effect on ramet survival and a positive effect on probability of flowering in *T. vulgare*. No other effect of age in any of the species was found.

### Relationships between the tussock-level parameters

All tussock-level parameters (number of neighbors, ramet position within tussock and tussock size) were significantly correlated at  $p < 0.001$ . However, the coefficients of determination were quite low. For the number of neighbors and position within the tussock the coefficients of determination was  $R^2 = 0.22$  for

*C. jacea* and 0.09 for *T. vulgare*. For the number of neighbors and size of tussock the coefficients of determination was  $R^2 = 0.11$  for *C. jacea* and 0.19 for *T. vulgare*.

## Discussion

### Effects of tussock-level parameters

The results show that the coefficients of determination between different tussock-level predictors are quite low (maximum 0.22 for ramet position and number of neighbors in *C. jacea*). Therefore all these predictors can be included into a single analysis without danger of over-parameterization. All the following results thus show pure effect of each parameter after adjusting for the effect of all the preceding ones.

True tussock-level parameters (namely age) had in some cases an effect on behavior of the ramets. Effect of tussock age was significant in *T. vulgare*, having a positive effect on the probability of flowering and a negative effect on ramet survival. This pattern may be indicative of senescence of larger tussocks. In contrast, there were no effects of this type in *C. jacea*. While the presence of perennial woody roots in both study plants may make senescence more important than in clonal plants (Falinska, 1995; Silvertown et al., 2001), clearly these two species differ in this respect. *T. vulgare*, a species of rather temporary habitats, shows signs of senescence, while *C. jacea*, a species of permanent mown meadows, does not. The latter species may be able to avoid senescence effects in a manner similar to clonal plants (e.g. De Kroon et al., 1991).

### Effects of position within the tussock and of local density

Effects of position within the tussock and local ramet density on ramet growth and survival were often rather strong. For position within a tussock we found both patterns: in *C. jacea* central ramets were doing better, while peripheral ramets were more successful in *T. vulgare*. While seeking an explanation for this phenomenon, it should be kept in mind that tests of the effects of number of neighboring ramets cannot separate intra-clonal regulation from pure competition of neighboring ramets. In all plants tested, the neighboring ramets are those that belong to the same tussock; this is due to the growth form of both species, where single tussocks are usually far apart from each other and most if not all interactions between ramets are within a tussock.

In *C. jacea*, central ramets had higher survival probabilities. *C. jacea* is a species of mown or grazed grasslands where competition for light is weaker both

**Table 2.** Summary table of results of tests of effect of tussock and ramet level parameters on total biomass, biomass of the inflorescence, and probability of flowering and survival in single ramets of *Tanacetum vulgare*

	Autumn biomass				Biomass of inflorescence			Flowering			Survival		
	d.f.	Error d.f.	F-value	P	Error d.f.	F-value	P	N	F-value	P	N	F-value	P
<i>Tussock-level variables</i>													
Locality	1	44	10.21	***	28	9.41	***	60	0.00	n.s.	100	0.97	n.s.
No. of fertile ramets	1	44	2.98	n.s.	28	12.83	*** (+)	60	3.40	n.s.	100	0.97	n.s.
No. of sterile ramets	1	44	3.86	n.s.	28	0.54	n.s.	60	6.28	** (–)	100	4.07	* (–)
Age	1	44	0.01	n.s.	28	0.38	n.s.	60	5.15	* (+)	100	12.12	*** (–)
Locality × no. of fertile <i>r</i>	1	44	6.64	*	28	9.25	**	60	0.45	n.s.	100	0.48	n.s.
Locality × no. of sterile <i>r</i>	1	44	1.06	n.s.	28	1.21	n.s.	60	1.49	n.s.	100	1.57	n.s.
Locality × age	1	44	1.81	n.s.	28	0.16	n.s.	60	0.24	n.s.	100	0.07	n.s.
<i>Ramet-level variables</i>													
Ramet height	1	100	14.36	*** (+)				108	2.14	n.s.	299	2.47	n.s.
Ramet diameter	1	100	6.69	* (+)				108	1.47	n.s.	299	0.02	n.s.
No. of leaves	1	100	1.47	n.s.				108	26.70	*** (+)	299	116.05	*** (+)
Autumn biomass of the ramet					30	85.55	*** (+)	108			299		
Position within tussock (proximity to the center)	1	100	0.3	n.s.	30	4.32	* (–)	108	3.11	n.s.	299	12.93	*** (–)
Ramet density	1	100	2.06	n.s.	30	0.62	n.s.	108	0.03	n.s.	299	0.65	n.s.
Locality × position within <i>t</i>	1	100	0.03	n.s.	30	0.61	n.s.	108	2.75	n.s.	299	0.19	n.s.
Locality × ramet density	1	100	4.38	*	30	0.95	n.s.	108	3.06	n.s.	299	6.78	**

Tests of autumn biomass and biomass of inflorescence were performed using analysis of covariance. Effects on probability of flowering and survival were tested using logistic regression. Two separate tests, one for variables defined at the level of tussock and one for those defined at the level of ramets, were used in this case. See methods for more detailed description of the tests. Signs in brackets indicate, where applicable, direction of significant relationships.

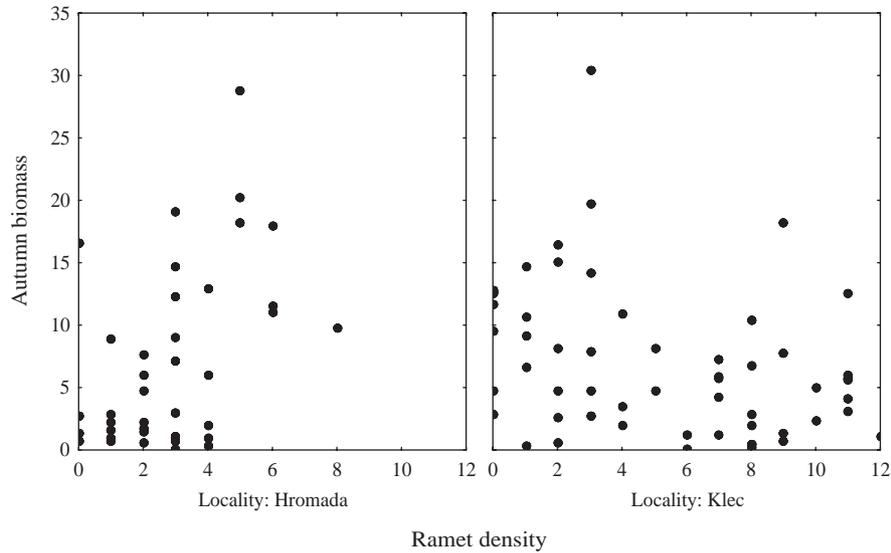
Results marked n.s. are non-significant, i.e.  $p > 0.05$ , \* stands for  $p > 0.01$ , \*\* for  $p > 0.001$ , \*\*\* for  $p \leq 0.001$ .

**Table 3.** Summary table of results of tests of effect of tussock and ramet level parameters on ramet diameter, ramet height, number of inflorescence and survival probability in single ramets of *Centaurea jacea*

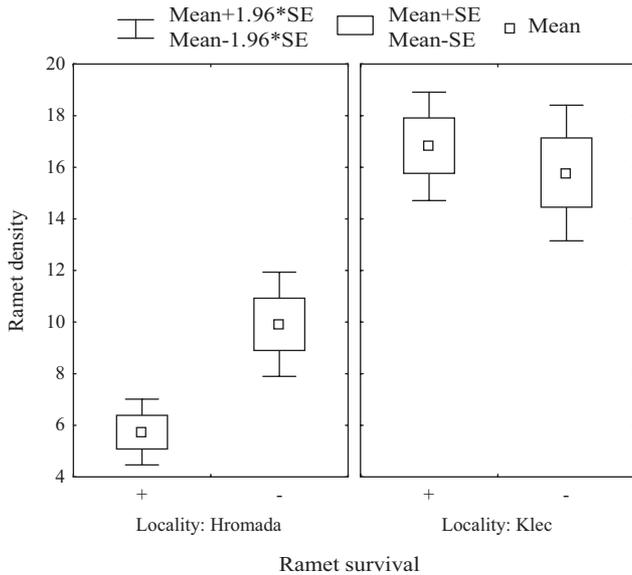
	Ramet diameter in autumn				Ramet height in autumn			Number of inflorescence			Survival		
	d.f.	Error d.f.	F-value	P	Error d.f.	F-value	P	Error d.f.	F-value	P	N	F-value	P
<i>Tussock-level variables</i>													
Locality	2	59	0.76	n.s.	59	13.24	***	46	1.56	n.s.	61	2.77	0.07
No. of fertile ramets	1	59	0.00	n.s.	59	19.08	*** (+)	46	1.48	n.s.	61	7.43	** (+)
No. of sterile ramets	1	59	4.64	* (+)	59	0.06	n.s.	46	0.01	n.s.	61	0.06	n.s.
Age	1	59	0.04	n.s.	59	0.01	n.s.	46	0.03	n.s.	61	0.6	n.s.
Locality × no. of fertile <i>r</i>	2	59	1.42	n.s.	59	0.92	n.s.	46	0.07	n.s.	61	1.48	n.s.
Locality × no. of sterile <i>r</i>	2	59	1.62	n.s.	59	2.24	n.s.	46	0.48	n.s.	61	1.03	n.s.
Locality × age	2	59	1.31	n.s.	59	1.62	n.s.	46	0.61	n.s.	61	2.69	n.s.
<i>Ramet-level variables</i>													
Ramet height in spring	1	84	2.01	n.s.	84	6.93	** (+)	62	4.02	* (+)	180	3.25	0.07
Ramet diameter in spring	1	84	9.83	*** (+)	84	0.71	n.s.	62	0.82	n.s.	180	1.69	n.s.
No. of leaves in spring	1	84	71.10	*** (+)	84	104.71	*** (+)	62	20.20	*** (+)	180	7.01	** (+)
Position within tussock (proximity to the center)	1	84	0.51	n.s.	84	0.76	n.s.	62	0.29	n.s.	180	25.41	*** (+)
Ramet density	1	84	0.15	n.s.	84	0.11	n.s.	62	0.01	n.s.	180	1.16	n.s.
Distance to the closest <i>r</i>	1	84	0.35	n.s.	84	0.47	n.s.	62	2.33	n.s.	180	0.89	n.s.
Locality × position within <i>t</i>	2	84	4.90	***	84	6.35	**	62	0.05	n.s.	180	0.83	n.s.
Locality × ramet density	2	84	0.21	n.s.	84	1.03	n.s.	62	0.13	n.s.	180	3.53	*
Locality × distance to the closest <i>r</i>	2	84	2.45	n.s.	84	2.80	n.s.	62	1.33	n.s.	180	11.86	***

Tests of ramet diameter and height in autumn and number of inflorescence were performed using analysis of covariance. Effects on probability of survival were tested using logistic regression. Two separate tests, one for variables defined at the level of tussock and one for those defined at the level of ramets, were used in this case. See methods for more detailed description of the tests. Signs in brackets indicate, where applicable, direction of significant relationships.

Results marked n.s. are non-significant, i.e.  $p > 0.05$ , \* stands for  $p > 0.01$ , \*\* for  $p > 0.001$ , \*\*\* for  $p \leq 0.001$ .



**Fig. 2.** Effect of ramet density on autumn biomass of ramets of *Tanacetum vulgare* at two different localities, low productive Hromada, and highly productive Klec. The overall effect of ramet density is not significant. There is however a strong interaction with the locality due to a significant positive effect at Hromada and no effect at Klec.



**Fig. 3.** Effect of ramet density on ramet survival of *Tanacetum vulgare* at two different localities, low productive Hromada, and highly productive Klec. The overall effect of ramet density is not significant. There is however a strong interaction with the locality due to a significant negative effect at Hromada and no effect at Klec. Sign ‘+’ in the graphs refers to the ramets that survived, ‘-’ refers to the ramets that died during the study period.

because of low productivity and disturbance by mowing. Central ramets also experience primarily intra-clonal competition, which might be reduced by intra-clonal density-regulation (Charpentier and Stuefer, 1999); in contrast, peripheral ramets experience mainly interspe-

cific competition. Position within the tussock might also determine ramet distance from the source of nutrients absorbed by the taproot which is usually located approximately in the center of the tussock (Briske and Butler, 1989; Derner and Briske, 1999). Still there was no effect of position on probability of flowering; ramet growth rate effects were not consistent among localities.

In contrast, in *T. vulgare* the ramets in the center survived and flowered less than ramets on the edge. This difference may be due to the fact that *T. vulgare* is much more a robust species that is likely to be a strong competitor for light. It also occurs at early successional habitats where the competition from other species is only gradually building up. Thus ramets at the edge are not likely to experience intensive inter-specific competition. On the other hand, ramets in the center may already be subjected to strong within-tussock competition. Moreover, dead last year ramets of *T. vulgare* often persist and thus further increase competition for space within tussocks.

In contrast to the effect of ramet position within tussock, the effect of tussock size and ramet density varied even between populations of the same species. These differences were found in both species, but they were particularly strong in *T. vulgare*. At the less productive Hromada site where ramets are smaller, higher number of close neighbors supported ramet growth; at the more productive location Klec, ramet growth was not effected by presence of other ramets in its surrounding. This is likely to be due to the interplay between the positive effect of overall tussock vitality which supports ramet growth with the negative effects of intra-tussock competition (Ishii and Takeda, 1997;

Mendoza and Franco, 1998; Suzuki and Hara, 2001), which is often supposed to be asymmetric (De Kroon et al., 1992). At the less productive habitat, only support of ramet growth is likely to be the dominant effect; at the more productive habitat, the non-significant effect may be a result of both these effects balancing each other. At the less productive Hromada site, ramet survival was, however, negatively affected by tussock size. This may be, e.g. due to higher ramet turnover in more vital tussocks, with more ramets (Eriksson, 1988). Similar, albeit weaker, effect of interaction between number of neighbors  $\times$  locality was also found for ramet survival in *C. jacea*.

Recent data show that combined positive and negative effects of neighbors in species interactions are commonplace in plants and often depend on the harshness of the environments (Callaway and Walker, 1997). In clonal plants, a reversed response of two ramet parameters to neighbor density was also found by Briske and Butler (1989) who demonstrated significant effects on ramet recruitment but not ramet survival in the tussock grass *Schizarium scoparium*. Change of the effect of position within the plant as a function of environment has also been reported by several other studies. Charpentier and Stuefer (1999) studied functional specialization of ramets of *Scirpus maritimus* based on ramet position within the genet and showed significant differences between three experimental ramet densities in the level of specialization. Dunlap et al. (1992) found locality  $\times$  position interaction in their study of resprouting ability of branches at different position within stems of *Populus trichocarpa*.

Our results are consistent with these findings as they show that both site- and species-specific effects of tussock level parameters can be identified. Clearly ramet performance is affected by many factors interacting at different levels. In particular, the parameters acting in the site-specific manner (such as tussock size) are likely to reflect different environmental conditions of these sites, namely different harshness that shifts the balance between negative and positive effects of neighbors within a tussock. The patterns in species-specific parameters (such as tussock age and ramet position within tussock) reflect differences in species life history traits.

However, the high variability in the responses found in this study also does not mean that such effects should be ignored. In contrast, no matter what process they result from, these effects may strongly interact with the overall size or fitness of the individuals, and their inclusion or omission may have a strong bearing on results of a demographic study. More studies are however needed to identify the environmental factors and life history traits responsible for the differences.

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## References

- Acosta, F.J., Serrano, J.M., Pastor, C., Lopez, F., 1993. Significant potential levels of hierarchical phenotypic selection in a woody perennial plant, *Cistus ladanifer*. *Oikos* 68, 267–272.
- Armstrong, R.A., 1982. A quantitative theory of reproductive effort in rhizomatous perennial plants. *Ecology* 63, 679–686.
- Armstrong, R.A., 1983. On the quantitative theory of resource partitioning in rhizomatous perennial plants: the influence of canopy structure, rhizome branching pattern, and self-thinning. *Ecology* 64, 703–709.
- Bishop, G.F., Davy, A.J., Jefferies, R.L., 1978. Demography of *Hieracium pilosella* in a breck grassland. *J. Ecol.* 66, 615–629.
- Briske, D.D., Butler, J.L., 1989. Density-dependent regulation of ramet populations within the bunchgrass *Schizarium scoparium*: interclonal versus intracolonial inference. *J. Ecol.* 77, 963–974.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Carlsson, B.A., Callaghan, T.V., 1990. Programmed tiller differentiation, intracolonial density regulation and nutrient dynamics in *Carex bigelowii*. *Oikos* 58, 219–230.
- Carlsson, B.A., Callaghan, T.V., 1991. Simulation of fluctuating populations of *Carex bigelowii* tillers classified by type, age and size. *Oikos* 60, 231–240.
- Charpentier, A., Stuefer, J.F., 1999. Functional specialization of ramets in *Scirpus maritimus*—splitting the tasks of sexual reproduction, vegetative growth, and resource storage. *Plant Ecol.* 141, 129–136.
- Cook, R.E., 1985. Growth and development of clonal plant populations. In: Jackson, J.B.C., Buss, L.W., Cook, R.E. (Eds.), *Population Biology and Evolution in Clonal Organisms*. Yale University Press, New Haven, pp. 259–296.
- Crawley, M.J., 1997. *Plant Ecology*, 2nd ed. Blackwell Science, Cambridge.

- Damman, H., Cain, M.L., 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *J. Ecol.* 86, 13–26.
- De Kroon, H., Whigham, D.F., Watson, M.A., 1991. Developmental ecology of mayapple—effects of rhizome severing, fertilization and timing of shoot senescence. *Funct. Ecol.* 5, 360–368.
- De Kroon, H., Hara, T., Kwant, R., 1992. Size hierarchies of shoots and clones in clonal herb monocultures—do clonal and nonclonal plants compete differently. *Oikos* 63, 410–419.
- Derner, J.D., Briske, D.D., 1999. Intraclonal regulation in a perennial cespitose grass: a field evaluation of above- and below-ground resource availability. *J. Ecol.* 87, 737–747.
- Dietz, H., Ullmann, I., 1997. Age determination of dicotyledonous herbaceous perennials by means of annual rings: exception or rule? *Ann. Bot.* 80, 377–379.
- Dunlap, J.M., Heilman, P.E., Stettler, R.F., 1992. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. 5. The influence of ramet position on 3-year growth variables. *Can. J. For. Res.* 22, 849–857.
- Eriksson, O., 1988. Ramet behaviour and population-growth in the clonal herb *Potentilla anserina*. *J. Ecol.* 76, 522–536.
- Falinska, K., 1995. Genet disintegration in *Filipendula ulmaria*: consequences for population dynamics and vegetation succession. *J. Ecol.* 89, 9–21.
- Harper, J.L., White, J., 1974. The demography of plants. *Annu. Rev. Ecol. Syst.* 5, 419–463.
- Hartnett, D.C., Bazzaz, F.A., 1985. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *J. Ecol.* 73, 407–413.
- Hossaert-Mc Key, M., Jarry, M., 1992. Spatial and temporal patterns of investment in growth and sexual reproduction in 2 stoloniferous species, *Lathyrus latifolius* and *L. sylvestris*. *J. Ecol.* 80, 555–565.
- Ishii, H., Takeda, H., 1997. Effects of the spatial arrangement of aerial stems and current-year shoots on the demography and growth of *Hydrangea hirta* in a light-limited environment. *New Phytol.* 136, 443–453.
- Mendoza, A., Franco, M., 1998. Sexual reproduction and clonal growth in *Reinhardtia gracilis* (*Palmae*), an understory tropical palm. *Am. J. Bot.* 85, 521–527.
- Němec, B., et al., 1962. *Botanická mikrotechnika*. ČSAV Praha (in Czech).
- Silvertown, J., Franco, M., Perez-Ishiwara, R., 2001. Evolution of senescence in iteroparous perennial plants. *Evol. Ecol. Res.* 3, 393–412.
- S-Plus 6 for Windows, 2001. Insightful Corporation. Seattle, WA.
- Suzuki, A., 2000. Patterns of vegetative growth and reproduction in relation to branch orders: the plant as a spatially structured population. *Trees Struct. Funct.* 14, 329–333.
- Suzuki, J.I., Hara, T., 2001. Partitioning of stored resources between shoots in a clone, and its effects on shoot size hierarchy. *Ann. Bot.* 87, 655–659.
- Thompson, D.A., Beattie, A.J., 1981. Density mediated seed and stolon production in *Viola* (*Violaceae*). *Am. J. Bot.* 68, 383–388.