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Stand structure and aboveground biomass partitioning in three populations of *Calamagrostis arundinacea*

Struktura porostů a distribuce nadzemní biomasy u tří populací *Calamagrostis arundinacea*

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Three populations of *Calamagrostis arundinacea*, i.e. a population developed in a dying forest and two populations on clearing sites (referred to as young and old) were studied in the area under air-pollution impact in the Moravian-Silesian Beskydy Mountains. A higher density of small tussocks (about 5 cm in diameter) was characteristic for the young clearing population. In the forest and old clearing populations larger tussocks (20-25 cm) were also present. The average total aboveground biomass was very low in the forest population (37 g.m^{-2}), while in the young and old clearing populations it was more than ten times higher (419 and 510 g.m^{-2}). Flowering shoots formed 3.3 and 8.1% of the total number of shoots and 10.8 and 21.4% of the aboveground biomass in the forest and old clearing populations, respectively. In the young clearing population in an open disturbed habitat, a larger percentage of biomass was allocated to flowering shoots and inflorescences represented, respectively, 74-84% and 7-8% of aboveground biomass of tussocks (5-15 cm in diameter). 55.4% of the aboveground stand biomass was formed by flowering shoots.

Introduction

The spread of expansive grasses, supported by changes in light conditions after deforestation, has been previously reported in areas under air-pollution impact, especially in mountains of Central Europe (e.g. Samek 1988, Fiala 1989, Fiala et al. 1989, Pyšek 1990). In these areas the forest dieback is linked with industrial activities resulting mainly in acidic depositions (Ulrich 1984, Materna 1986, Pitelka et Raynal 1989, Schulze et al. 1989). Besides the vast stands of *Calamagrostis villosa* that replace original spruce (*Picea abies*) forests, *Calamagrostis arundinacea*, another expansive plant species, covers large tracts of clearings namely in places of original mountainous beech (*Fagus sylvatica*) or spruce-fir-beech (*Picea abies-Abies alba-Fagus sylvatica*) forests on soils with poor or medium supply of nutrients (Zelená 1994). These grasses often form almost monospecific

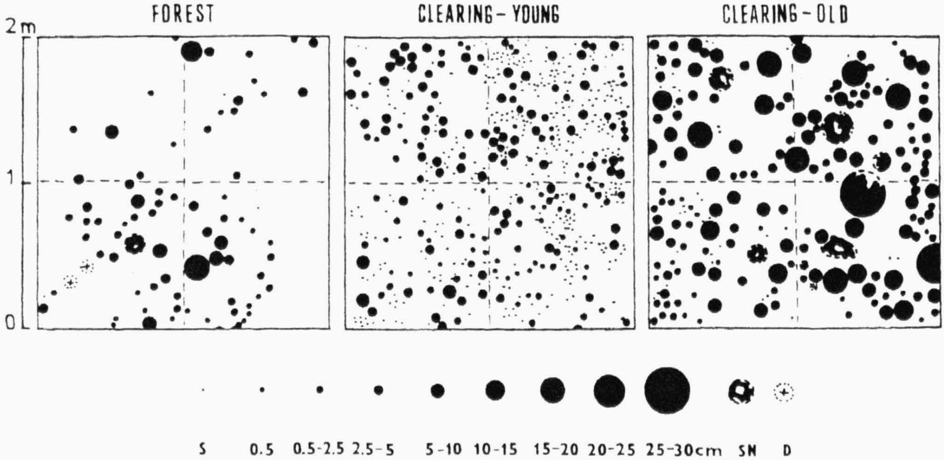

Fig. 1. - The spatial pattern of *Calamagrostis arundinacea* tussocks in forest, young and old clearing populations; horizontal projection of tussock bases: 0.5, 0.5 - 2.5 cm, etc. - different size categories, S - seedlings, SN - senescent tussocks, D - dead tussocks.

stands of different developmental stage on deforested sites. *C. villosa* spreads intensively by the growth of its rhizomes in reached habitats (Slavoňovský 1957, Lokvenc 1971, Fiala 1989, Lipnická-Morávková 1991). On the contrary, *C. arundinacea* reproduces and spreads mostly by seeds (Rychnovská et al. 1990, Fiala et al. 1994).

The plant reproductive effort (percentage of total energy or biomass spent on reproduction - see Harper et Ogden 1970) is partly a fixed genetic trait but it can be modified by the environment. Higher reproductive effort has been reported for populations in a harsh open habitat or in dry, disturbed, pioneer sites than for those in moderate habitats (Solbrig et Simpson 1974, Hickman 1975, Sterk 1975, Seischab et al. 1985). Generally the total allocation of resources to sexual reproduction is much greater in resource-rich than in resource-poor environments (Bloom et al. 1985). Vegetative reproduction is emphasized at the expense of sexual reproduction in more severe climates (cf. Douglas 1981). Seed production usually declines with increasing competition (Ogden 1974, Ernst 1979, Lee et Hamrick 1983, Smith 1983, Hartnett et Bazzaz 1985), while nutrients are more limiting under crowding. The density alone is an inadequate predictor of reproductive effort. Successional status, environmental conditions and persistence strategy (ability to survive or reproduce in shade) must also be considered (Loehle 1987). In addition, sexual reproduction differs greatly from year to year (Bloom et al. 1985, Inghe et Tamm 1988, Ohlson 1988, de Jong et Klinkhamer 1989, Carlsson and Callaghan 1990). Callaghan et al. (1992) pointed out that we still have a very poor understanding of the processes of trade-off between sexual and vegetative reproduction of clonal plants and what controls them and what the environmental and innate cues are for flowering.

The aim of this study was to examine the variability in reproductive allocation of several *C. arundinacea* populations. By concentrating on the pattern of biomass partitioning, we provide new data on the sexual reproductive ability of *C. arundinacea* and the possibility of its spreading into newly formed deforested sites in the process of secondary succession following the air-pollution damage of forest.

Study sites and methods

Study sites

Study sites were situated near the top of the Malý Smrk Hill (49°31' N, 18°24' E, altitude ca. 1100 m) about 35 km south-east of the town of Ostrava in the Moravian-Silesian Beskydy Mountains. The region is characterized by annual mean air temperature of about 5°C (2.9°C for the top of the Smrk Hill, i.e. the altitude of 1276 m) and average annual precipitation of 1200 mm (Buzek et al. 1986). The following populations of *Calamagrostis arundinacea* were studied: (i) a population developed in a dying spruce forest (referred to as the forest population), (ii) a young, clearing population on an area deforested by air-pollution (the young clearing population), and (iii) an old population also growing on a deforested area (the old clearing population). The forest population of *Calamagrostis arundinacea* occurred in a spruce monoculture (about 40 years old; 23 % of the trees have died or are damaged) on east-facing slope (ca. 30°). The stand was not closed and consisted of dispersed individual tussocks (Fig. 1). No other plant species were present in this site. Study sites with both young and old clearing *C. arundinacea* populations were situated on a northeast-facing slope (ca. 15°) deforested by felling of damaged spruce stands in 1982-1983, i.e. the clearing was five to six years old. The young population (about five year old, Fig. 1) was developed on a disturbed area probably created under the influence of both transportation of trunks and water erosion, on sites with stony, shallow soil and lower organic matter content in the uppermost soil layer (Table 1). The stand of the old *C. arundinacea* population represented a closed vegetation cover of the deforested area (Fig. 1) and was dominated by *C. arundinacea*, covering up to 96% of the area. Amongst other plant species, *Deschampsia flexuosa, Oxalis acetosella, Rubus idaeus, Vaccinium myrtillus*, and *Dryopteris dilatata* (nomenclature according to Tutin et al. 1964-1980) occurred more frequently in the stands of both young and old clearing populations. The substrate of the study sites is medium deep to shallow humic sandy loamy soil (podsol), acidic, rich in gravel, and poor in nutrients, developing on sandstones. Chemical features of the soils are given in Table 1. A higher content of calcium in top soil layers can be accounted for by the aerial application of ground dolomite on the clearings.

Aboveground biomass sampling

Aboveground biomass was sampled on August 24, 1988. In each site, the total aboveground plant material produced in the current year (excluding plant litter) was harvested from five 0.5 × 1.0 m plots. In addition, 105 tussocks (genets, see Harper 1977, Falińska 1986) were sampled randomly outside the harvested plots (including underground shoot bases)

Table 1. - Characteristics of the sites studied: pH, exchangeable cations, C and N contents in the 0 - 5 cm (a), 5 - 10 cm (b) and 10 - 15 cm (c) soil layers of *Calamagrostis arundinacea* populations. All contents related to dry mass. Recorded on September 26, 1990.

Populations		pH (H_2O)	pH (KCl)	Ca^{2+}	Mg^{2+}	Al^{3+}	C	N
				(mg.kg^{-1})			(%)	
Forest	a)	3.72	2.87	1522	322	937	31.4	1.33
	b)	3.61	2.71	220	310	823	18.8	0.82
	c)	3.46	2.72	60	243	701	13.4	0.63
Clearing - young	a)	4.61	3.54	1822	450	384	14.2	0.67
	b)	3.90	2.77	200	237	668	6.9	0.32
Clearing - old	a)	4.20	3.50	2833	821	283	26.0	1.18
	b)	3.60	2.72	230	207	721	7.7	0.39
	c)	3.87	2.84	80	134	735	4.8	0.30

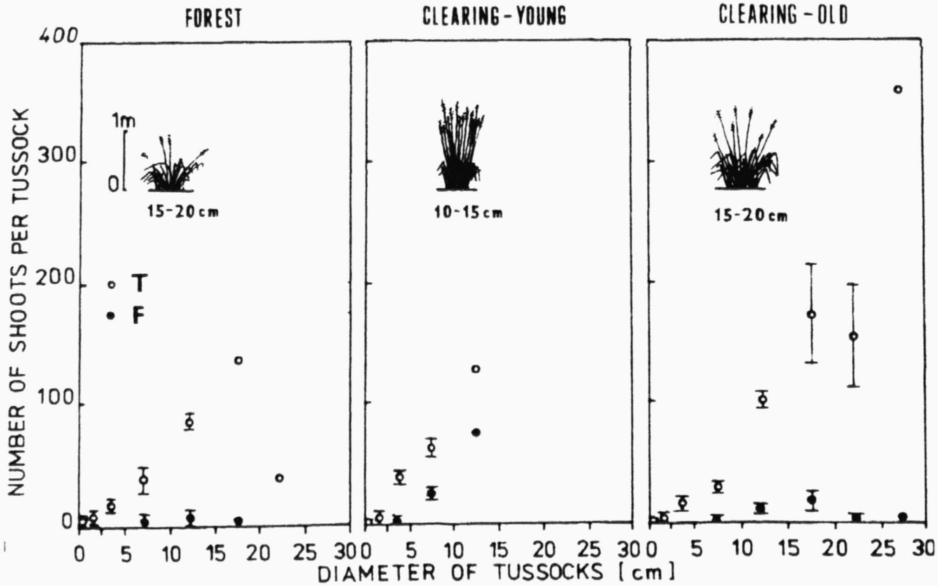

Fig. 3. - The number of total (T) and flowering shoots (F) in different size categories of *Calamagrostis arundinacea* tussocks in forest, young and old clearing populations. Mean values are presented ± 1 S.E. where available. Tusssocks are shown schematically in top parts.

to obtain several samples of all size categories present in the studied populations (Table 2). Each of these tussocks was brought back to the laboratory, its diameter was measured at the tussock base, aboveground parts separated, and number of vegetative and flowering shoots counted. The aboveground parts of stands collected from harvest plots were separated into vegetative and flowering shoots, and the length of all individual vegetative shoots, flowering shoots and inflorescences was measured. All plant material was dried at 70-80 °C and the biomass of vegetative shoots, flowering shoots and inflorescences was weighed separately.

The number of tussocks of different sizes (measured as a diameter at the tussock base) and the number of seedlings of *C. arundinacea* were counted in one 2 × 5 m plot in each site on May 18-19, 1988.

Soil and statistical analyses

Chemical analyses of the mixed soil sample from each site (Table 1) were accomplished by the following methods: pH in H_2O and 1 N KCl extracts (electrometrical method), exchangeable cations Ca^{2+}, Mg^{2+} and Al^{3+} in the 1 N KCl extract using complexometric titration (Moravec 1960), total C and N by elemental analyzer CHN 1106 (Carlo Erba).

The data were analysed using standard statistical methods. The differences between populations were tested using ANOVA.

Results

A high number of small tussocks and absence of larger ones was typical for the young clearing population (Fig. 2). In this population, 67 seedlings per m^2 were recorded (Fig. 1). The old clearing population consisted of numerous small tussocks as well, but larger tussocks were frequently present. No tussocks larger than 20 cm in diameter were found in the forest population. Some of the smaller tussocks had degenerated (senescent), as evident from a gap in their middle part, and some of them were already dead (Fig. 1). The mean number of seedlings was 31.8 and 1.7 per m^2 in the old clearing and forest populations, respectively.

A comparison of tussocks of the same size category across all studied populations showed that most of the tussocks of the young clearing population had the greatest total number of vegetative and flowering shoots (Fig. 3). The number of flowering shoots decreased in tussocks larger than 20 cm in diameter both in the old clearing and the forest populations (even in tussocks smaller than 20 cm in the latter). In the young clearing population, the number of flowering shoots conspicuously increased with tussock size. The percentages of flowering shoots went up to 27% and even 76% in the tussocks of 5-10 cm and 10-15 cm in diameter, respectively.

Much greater differences were observed among tussocks from the three sites when expressed as grams of dry mass of the aboveground biomass per cm of tussock diameter

Table 2. – Average aboveground biomass (in g) of *Calamagrostis arundinacea* tussocks of different size categories. Percentages of the total biomass are also given. Standard errors are shown in parentheses.

	Tussock diameter (n cm)							
	<0.5	0.5–2.5	2.5–5.0	5–10	10–15	15–20	20–25	25–30
Forest population								
Vegetative shoots	0.025 (0.006) 100%	0.22 (0.03) 100%	0.81 (0.11) 100%	4.61 (1.04) 78.8%	11.13 (2.4) 83.9%	17.59 91.9%	6.82 100%	– –
Flowering shoots	0 (0.62) 21.2%	0 (0.86) 16.1%	0 8.1%	1.24 0	2.14 –	1.56	0	–
Inflorescences	0 (0.05) 2.7%	0 (0.12) 2.3%	0 1.1%	0.16 0	0.30 –	0.21	0	–
Total biomass	0.025 (0.006)	0.22 (0.03)	0.81 (0.11)	5.85 (1.10)	13.27 (2.4)	19.15	6.82	–
n	3	14	9	13	6	2	2	
Young clearing population								
Vegetative shoots	0.03 (0.09) 100%	0.28 (0.44) 100%	2.78 (1.1) 90%	6.01 25.1%	11.75 16.3%	– –	– –	– –
Flowering shoots	0 (0.16) 10%	0 (2.6) 74.9%	0.31 83.7%	17.97 –	60.44 –	– –	–	–
Inflorescences	0 (0.01) 0.7%	0 (0.29) 6.9%	0.02 7.7%	1.66 –	5.53 –	– –	–	–
Total biomass	0.03 (0.09)	0.28 (0.51)	3.09 (3.0)	23.98	72.19	–	–	–
n	2	9	8	11	2	–	–	–
Old clearing population								
Vegetative shoots	0.25 (0.11) 100%	0.57 (1.5) 100%	3.72 (1.2) 100%	8.71 (4.9) 90.5%	31.16 (17.8) 77.4%	50.47 (26.6) 68.8%	61.87 93.0%	107.80 95.3%
Flowering shoots	0 (0.6) 9.5%	0 (2.7) 22.6%	0 (12.7) 31.2%	0.92 (2.2) 7.0%	9.10 4.7%	22.87	4.64	5.35
Inflorescences	0 (0.02) 0.5%	0 (0.36) 1.7%	0 (0.65) 3.6%	0.05 (0.40) 0.8%	0.69 0.7%	2.65	0.53	0.8
Total biomass	0.25 (0.11)	0.57 (1.5)	3.72 (2.0)	9.63 (7.4)	40.26 (13.0)	73.34 (25.9)	66.51	113.15
n	2	4	4	4	3	3	3	1

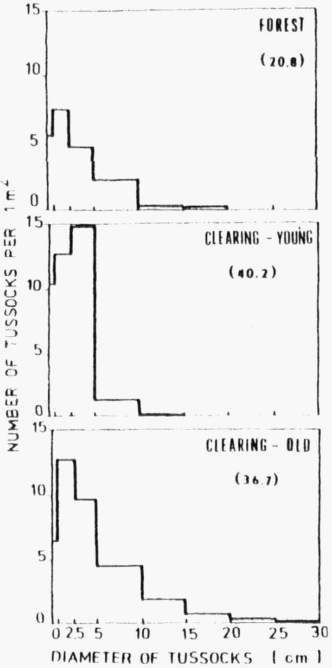

Fig. 2. - Number of *Calamagrostis arundinacea* tussocks of different size categories in forest, young and old clearing populations. Total number of tussocks per 1 m^2 is in parentheses.

(Fig 4). In tussocks smaller than 5 cm in diameter in the forest and old clearing populations, all aboveground biomass was vegetative. In the forest population, about 16% of the total biomass was accounted for by the flowering shoots in tussocks 10-15 cm in size. In tussocks 15-20 cm in size of the old clearing population, flowering shoots represented about 31% the total aboveground biomass. The biomass of flowering shoots decreased and a smaller proportion of the aboveground biomass was allocated to flowering shoots in larger tussocks of both the forest and old clearing populations (Fig. 4). Further increase in the total aboveground biomass was not observed.

The increase of the aboveground biomass of tussocks was highest in the young clearing population, reaching nearly twice the value it displays in the same size categories of the old clearing population (Fig. 4). The biomass of flowering shoots in these two populations attained about 75 and 84% of the total aboveground biomass, respectively. The mean dry mass of inflorescences reached on itself about 6.9 to 7.7% of the total aboveground biomass, i.e. values 13.8 and 4.5 times as high as in the old clearing population (Fig. 4, Table 2). Differences in structure and formation of tussocks are, consequently, reflected in density and aboveground biomass partitioning of the three *Calamagrostis arundinacea* populations studied (Table 3). The stand of the forest population was very sparse (123 shoots per m^2). Individual tussocks were dispersed mainly over gaps in the dying forest stand. The average total aboveground biomass was also very low (37 g.m^{-2}) in comparison with the young (419 g.m^{-2}) and old clearing (510 g.m^{-2}) populations. The total shoot density of both young and old clearing populations attained more than 300 shoots per m^2. Flowering shoots represented approximately 3.3 and 8.1% of the total number of shoots in the forest and old clearing populations, respectively (Table 3). However, about 24% of flowering shoots (88 shoots per m^2) were recorded in the young clearing population. The largest proportion of aboveground biomass was represented by vegetative shoots in the forest (89.2%) and old clearing populations (78.6%). The biomass of shorter vegetative shoots of the young clearing population corresponded to less than a half of the biomass of all vegetative shoots of the old clearing population (Table 3). More than 50% of the aboveground biomass of the young clearing population was thus allocated to produce flowering shoots.

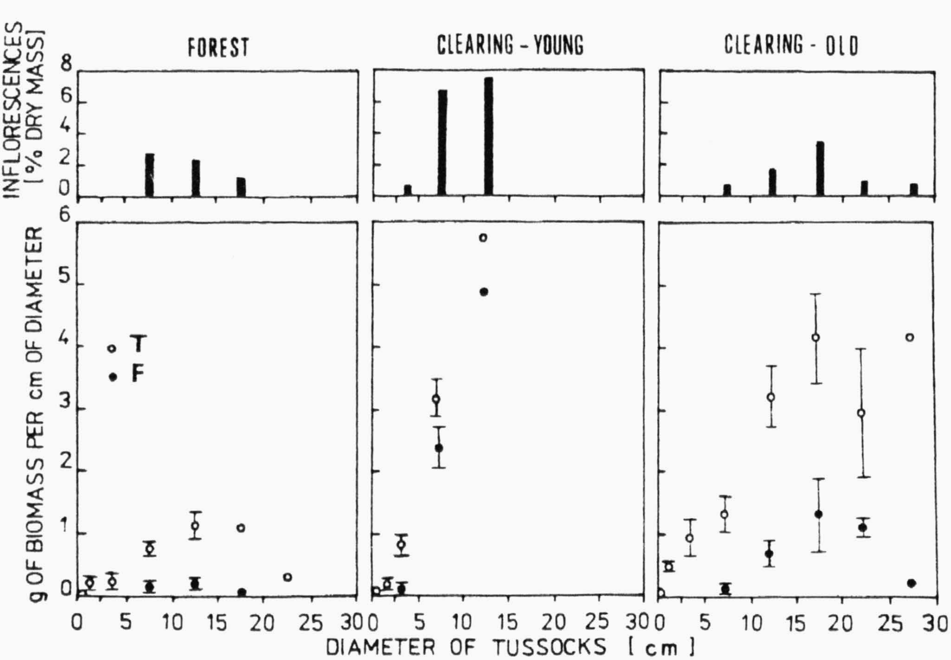

Fig. 4. - Relationship between the biomass of total (T) and flowering (F) shoots and the proportion of biomass allocated to inflorescences in *Calamagrostis arundinacea* tussocks of different size categories in forest, young and old clearing populations. Mean values are presented ± 1 S.E. where available.

Discussion

The present study documented, that the reproductive allocation in *C. arundinacea* changes with plant age. The greatest reproductive effort was found amongst those sedge or grass tussocks which had passed the point of maximum aboveground growth rate (Bernard et Fiala 1986, Mitka 1989). This was also observed in the *C. arundinacea* populations studied. A decline in number of flowering shoots and aboveground biomass was recorded in tussocks larger than 20 cm in diameter in the forest and old clearing populations (Fig. 4). This indicates that further increase in size of tussocks of both populations is not probably. Shoot natality is negatively density-dependent and shoot mortality increases with increasing clone density (Hartnett et Bazzaz 1985, Lapham et Drennan 1987, Briske et Butler 1989, de Kroon et Kwant 1991). Similarly, in old mature tussocks, shoot crowding causes their higher mortality. Tiller density per unit area of *Eriophorum vaginatum* tussock also declined with increasing diameter, and tiller size and the intensity of new tiller production were related to tussock diameter (Shaver et al. 1986). The reproduction may be delayed until the plant reaches such a size as to be able to survive, or at least to complete its first attempt

Table 3. - The mean values of shoot density (number of shoots per 1 m^2), aboveground biomass (in g of dry mass per 1 m^2), length of shoots and panicles (in cm) in *Calamagrostis arundinacea* populations. Percentages are also given. Standard errors are shown in parentheses. Means followed by the same letter row-wise were not significantly different at $P = 0.05$ (ANOVA test).

	Forest	Clearing	
		Young	Old
Shoot density			
Vegetative shoots n=5	119^{a}(21.3) 96.7%	278^{b}(24.3) 76.0%	306^{b}(36.3) 91.9%
Flowering shoots n=5	4^{a}(1.4) 3.3%	88^{b}(13.0) 24.0%	27^{a}(8.7) 8.1%
Total shoots n=5	123^{a}(21.3)	366^{b}(24.5)	333^{b}(40.3)
Shoot length			
Vegetative shoots n	30.0^{a}(0.5) 634	34.1^{b}(0.4) 1362	52.1^{c}(0.3) 2011
Flowering shoots n	51.9^{a}(2.8) 19	84.4^{b}(1.2) 347	92.1^{c}(1.9) 138
Panicle length n	11.4^{a}(0.5) 19	11.6^{a}(0.2) 347	15.1^{b}(0.3) 138
Aboveground biomass			
Vegetative shoots n=5	33^{a}(3.3) 89.2%	187^{b}(40.2) 44.6%	401^{c}(22.8) 78.6%
Flowering shoots n=5	4^{a}(1.1) 10.8%	232^{c}(35.7) 55.4%	109^{b}(36.4) 21.4%
Total biomass n=5	37^{a}(4.2)	419^{b}(51.2)	510^{b}(40.8)

at reproduction. On the other hand, high mortality risks at any stage of the life history favour early reproduction (Silvertown 1982).

In the clearing sites, a greater biomass of vegetative shoots was recorded in the old population growing in relatively nutrient-richer conditions. However, the number and proportion of flowering shoots in tussocks and in the aboveground biomass of the young population (in disturbed, nutrient-poor habitat) were probably at least twice as high as in other populations studied. Similarly, Jakrlová (1989) reported that 50% of the aboveground biomass was allocated to flowering shoots in another *C. arundinacea* stand on a deforested slope of the Malý Smrk Hill in the Moravian-Silesian Beskydy Mountains. In this stand, the total aboveground biomass was over 500 g.m^{-2} (Jakrlová 1989) and the total underground biomass attained 2021 g.m^{-2} (Fiala 1989). Studies of the *Calamagrostis villosa* stands - another plant species dominated on deforested areas - indicate that their total aboveground biomass can also reach high values (300-700 g.m^{-2}) and even exceed 1000 g.m^{-2} (Fiala et al. 1989, Jakrlová 1989, Lipnická-Morávková 1991, Pyšek 1991, 1993, Zelená, unpublished data).

Interpopulation differences in seed allocation may arise from differences in the nature or the availability of that particular resource that limits the reproductive allocation of biomass, and do not necessary reflect differences in partitioning strategies (Schat et al. 1989). Van Andel et Vera (1977) found that proportional sexual reproductive effort in *Epilobium angustifolium* increased with increasing soil fertility. Application of nutrients to a dense population can partially reverse the negative effect of density on the reproductive effort (Snell et Burch 1975). In a contrasting study, the mineral fertilization had no significant effect on the average number of flowering stems per *Molinia arundinacea* tussock, regardless of size-classes (Mitka 1989). Plants transplanted to xeric sites had higher reproductive effort than plants transplanted to mesic sites (Platenkamp et Foin 1990). In dunes, on the contrary, watering raised total seed mass by 50% (Klinkhamer and de Jong 1993). Stress due to summer drought may affect the probability of flowering in the next year (Inghe et Tamm 1985, 1988). In resource-poor environments, intensive reproduction generally occurs in mast crops following the year of favourable conditions (Bloom et al. 1985). Flowering of *Carex bigelowii* varied greatly between years in Swedish Lapland (Carlsson and Callaghan 1990). Ohlson (1988) also reported on the mean reproductive effort of *Saxifraga hirculus* ramets being highly variable from year to year. A phenotypic plasticity is one possible explanation for the variable results in different studies of perennial plants (Syrjanen et Lehtila 1993).

As to the data on the number of florets in inflorescences (panicles) in the three populations analysed in the present paper (Novotná J., unpublished data), the number of seeds may be estimated at 600 per m^2 in the forest, 19 000 in the young clearing, and 11 000 in the old clearing populations. The decrease in sexual reproductive effort under less favourable light conditions was observed in several plant populations (Barkham 1980, Towpasz et Szymska 1983, Solbrig et al. 1988, Pyšek 1991). The role of generative reproduction also declines progressively in the course of succession (Newell et Tramer 1978, Fekete et Melkó 1981, Soukupová 1984, Pyšek 1992). Local recruitment from seed is generally low in closed stands of most clonal species. However, it occurs in clonal plants of forest understorey vegetation and in disturbed habitats (Beasleigh et Yarranton 1974, Seischab et al. 1985, Eriksson 1989, Jonasson 1992). Eriksson (1992) has found that majority (60%) of species do not establish adult populations from seed. Thus the seedlings may initiate the development of a patch, but do not appear to contribute substantially to the population dynamics after the initial colonization event.

Our results correspond to most of the data and conclusions of the above-mentioned authors. The biomass partitioning in *C. arundinacea* populations, particularly in flowering shoots and panicles, appears to depend not only on the age structure of populations, but also on adaptive responses to site conditions. The following hypothesis may explain the high sexual reproduction in *C. arundinacea* populations: In open habitats, i.e. under the conditions of low competitive stress, and in the harsh environment of disturbed pioneer sites newly created after deforestation, *C. arundinacea* exhibits the R-strategy characteristics (Grime 1979). This is reflected by larger percentage of biomass allocated to generative reproduction in the young population growing in such areas in the Moravian-Silesian Beskydy Mountains.

This fact could be very important for further intensive spread of *C. arundinacea* into open clearings where it rapidly forms close and dense vegetation cover and protects disturbed areas efficiently against soil erosion because of its aboveground biomass and extensive root system (Fiala 1989).

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Souhrn

Tři populace *Calamagrostis arundinacea* (lesní populace, mladá a stará populace na mýtině) byly studovány v oblasti s imisní zátěží v Moravskoslezských Beskydech. Rozdíly byly nalezeny v hustotě prýtů, v nadzemní biomase, ve věkové struktuře populací a ve vytváření trsů. V mladé populaci na mýtině (po těžbě narušené půdní erozí) bylo větší procentuální množství nadzemní biomasy využíváno ke generativní reprodukci. Kvetoucí prýty představovaly 74-84% (květenství 7-8%) nadzemní biomasy trsů a 55.4% nadzemní biomasy porostu.

References

Barkham J. P. (1980): Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed reproduction, mortality and the effect of density. - J. Ecol., Oxford, 68:607-633.

Beasleigh W.J. et Yarranton G. A. (1974): Ecological strategy and tactics of *Equisetum sylvaticum* during a postfire succession. - Can. J. Bot., Ottawa, 152:2299-2318.

Bernard J. M. et Fiala K. (1986): The life history strategy reflected in standing crop and biomass allocation patterns of *Carex comosa* Boot: a clump forming wetland sedge. - Ekológia (ČSSR), Bratislava, 5:247-259.

Bloom A. J., Chapin F. S. et Mooney H. A. (1985): Resource limitation in plants - an economic analogy. - Ann. Rev. Ecol. Syst., Palo Alto, 16:363-392.

Briske D. D. et Butler J. L. (1989): Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium*: interclonal versus intraclonal interference. - J. Ecol., Oxford, 77:963-974.

Buzek L. et al. (1986): Beskydy. Příroda a vztahy k ostravské průmyslové oblasti. - 347 p., ed. Pedagogická fakulta, Ostrava.

Callaghan T. V. et al. (1992): Clonal plants and environmental changes: introduction to the proceedings and summary. - Oikos, Copenhagen, 63:341-347.

Carlsson B. A. et Callaghan T. V. (1990): Effect of flowering on the shoot dynamics of *Carex bigelowii* along an altitudinal gradient in Swedish Lapland. - J. Ecol., Oxford, 18:152-165.

de Kroon H. et Kwant R. (1991): Density-dependent growth responses in two clonal herbs: regulation of shoot density. - Oecologia, Berlin, 86:298-304.

Douglas D. A. (1981): The balance between vegetative and sexual reproduction of *Mimulus primuloides* (*Scrophulariaceae*) at different altitudes in California. - J. Ecol., Oxford, 69: 295-310.

Eriksson O. (1989): Seedling dynamics and life histories in clonal plants. - Oikos, Copenhagen, 55:231-238.

Eriksson O. (1992): Evolution of seed dispersal and recruitment in clonal plants. - Oikos, Copenhagen, 63:439-448.

Ernst W. H. O. (1979): Population biology of *Allium ursinum* in northern Germany. - J. Ecol., Oxford, 67:347-362.

Falińska K. (1986): Pojecie osobnika w demografii roślin. - Wiadom. Ekol., Warszawa, 32:361-380.

Fekete G. et Melkó E. (1981): Reproductive allocation in the stages of sandy succession. - Acta Bot. Acad. Sci. Hung., Budapest, 27:351-364.

Fiala K. (1989): Underground biomass of three typical grass stands growing on areas deforested by air-pollution. - Ekológia (ČSSR), Bratislava, 8:105-115.

Fiala K., Jakrlová J. et Zelená V. (1989): Biomass partitioning in two *Calamagrostis villosa* stands on deforested sites. - Folia Geobot. Phytotax., Praha, 23:207-210.

Fiala K., Zelená V. et Jakrlová J. (1994): Struktura a produkce porostů s dominantními druhy rodu *Calamagrostis* na imisních holinách. - Zpr. Čes. Bot. Společ., Praha, 28 (Suppl. 13) [in print].

Grime J. P. (1979): Plant strategies and vegetation processes. - 222 p., John Wiley & Sons etc.

Hartnett D. C. et Bazzaz F. A. (1985): The regulation of leaf, ramet and genet densities in experimental populations of the rhizomatous perennial *Solidago canadensis*. - J. Ecol., Oxford, 73:429-443.

Harper J. L. (1977): Population biology of plants. - 892 p., Academic Press, New York.

Harper J. L. et Ogden J. (1970): The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris*. - J. Ecol., Oxford, 58:681-698.

Hickman J. C. (1975): Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense*. - J. Ecol., Oxford, 63:689-701.

Inghe O. et Tamm C. O. (1985): Survival and flowering of perennial herbs. IV. The behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots 1943-1981. - Oikos, Copenhagen, 48:400-420.

Inghe O. et Tamm C. O. (1988): Survival and flowering of perennial herbs. V. Patterns of flowering. - Oikos, Copenhagen, 51:203-219.

Jakrlová J. (1989): Úloha travinných porostů s *Calamagrostis* sp. v imisní oblasti Beskyd. - In: Gáborčík N. [red.], Ekológia trávneho porastu III., p. 192-201, ed. Dom techniky ČSVTS, Banská Bystrica.

Jonasson S. (1992): Plant responses to fertilization and species removal in tundra related to community structure and clonality. - Oikos, Copenhagen, 63:420-429.

Jong T. J. de et Klinkhamer G. L. (1989): Limiting factors for seed production in *Cynoglosum officinale*. - Oecologia, Berlin, 80:167-172.

Klinkhamer P. G. L. et de Jong T. J. (1993): Phenotypic gender in plants: effects of plant size and environment on allocation to seeds and flowers in *Cynoglossum officinale*. - Oikos, Copenhagen, 67:81-86.

Lapham J. et Drennan D. S. H. (1987): Intraspecific regulation of populations of the clonal herb, *Cyperus esculentus*. - J. Appl. Ecol., Oxford, 24:1011-1024.

Lee J. M. et Hamrick J. L. (1983): Demography of two natural populations of musk thistle (*Carduus nutans*). - J. Ecol., Oxford, 71:923-936.

Loehle C. (1987): Partitioning of reproductive effort in clonal plants: a benefit-cost model. - Oikos, Copenhagen, 49:199-208.

Lokvenc T. (1971): Vliv rostlinných společenstev na růst kleče. - Opera Corcont., Praha, 7-8:125-140.

Materna J. (1986): An outlook in the influence of air-pollution on forests in the ČSR. - Lesnictví, Praha, 32:319-328.

Mitka J. (1989): Effect of mineral fertilization upon the forest grass population of *Molinia arundinacea* Schrank. II. Population flux and reproductive effort. - Zesz. Nauk. UJ, Prace Bot., Kraków, 18:95-112.

Moravec J. (1960): Komplexometrické stanovení výměnných iontů - Ca^{++}, Mg^{++}, Al^{+++}, H^+ v bezkarbonátových půdách. - Sborn. ČSAZV, Rostl. Výr., Praha, 6:1015-1024.

Morávková-Lipnická K. (1991): Ekologie třtiny chloupkaté (*Calamagrostis villosa* (Chaix) J.F.Gmelin) v imisně postižené oblasti Jizerských hor. - Thesis, [depon. in: Dept. Bot. Charles Univ., Prague.]

Newell S. J. et Tramer E. J. (1978): Reproductive strategies in herbaceous plant communities during succession. - Ecology, Durham, 59:228-234.

Ogden J. (1974): The reproductive strategy of higher plants. II. The reproductive strategy of *Tussilago farfara* L. - J. Ecol., Oxford, 62:291-324.

Ohlson M. (1988): Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. - J. Ecol., Oxford, 76:1007-1016.

Pitelka L. F. et Raynal D. J. (1989): Forest decline and acidic depositions. - Ecology, Durham, 70:2-10.

Platenkamp G. A. J. et Foin T. C. (1990): Ecological and evolutionary importance of neighbours in the grass *Anthoxanthum odoratum*. - Oecologia, Berlin, 83:201-208.

Pyšek P. (1990): The influence of *Calamagrostis villosa* on the species diversity of deforested sites in the Krušné hory Mts. - Preslia, Praha, 62:323-335.

Pyšek P. (1991): Biomass production and size structure of *Calamagrostis villosa* populations in different habitats. - Preslia, Praha, 63:9-20.

Pyšek P. (1992): Dominant species exchange during succession in reclaimed habitats: a case study from areas deforested by air pollution. - Forest Ecol. Manag., Amsterdam, 54:27-44.

Pyšek P. (1993): What do we know about *Calamagrostis villosa*? - A review of the species behaviour in secondary habitats. - Preslia, Praha, 65:1-20.

Rychnovská M., Fiala K. et Květ J. (1990): Non-production functions of grassland. - In: Gáborčík N. et Krajčovič V. [red.], Soil - grassland - animal relationships, Proceedings of 13th General meeting of the European Grassland Federation, 25. - 29. 6. 1990, Vol. 1, p. 88-102, Banská Bystrica.

Samek V. (1988): Expanze třtiny chloupkaté v imisních oblastech hor. - Živa, Praha, 36:45-46.

Slavoňovský F. (1957): Mechanické vlastnosti kořenů některých rostlin svážných území Jeseníku. - Spisy Přír. Fak. MU, Brno, 381:1-68.

Schat H., Ouborg J. et de Wit R. (1989): Life history and plant architecture: size-dependent reproductive allocation in annual and biennial *Centaurium* species. - Acta Bot. Neerl., Wageningen, 38:183-201.

Shaver G. R., Chapin F. et Gartner B. L. (1986): Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. - J. Ecol., Oxford, 74:257-278.

Schulze E. D., Lange O. L. et Oren R. [red.] (1989): Forest decline and air pollution. A study of spruce (*Picea abies*) on acid soils. - Ecol. Stud., Berlin et Heidelberg, 77:1-475.

Seischab F. K., Bernard J. M. et Fiala K. (1985): Above- and belowground standing crop partitioning of biomass by *Eleocharis rostellata* Torr. in the Byron-Bergen Swamp, Genesse County, New York. - Amer. Nat., Notre Dame, 114:70-76.

Silvertown J. W. (1982): Introduction to plant population ecology. - 209 p., ed. Longman House, London et New York.

Smith B. H. (1983): Demography of *Floerkea proserpinacoides*, a forest-floor annual. II. Density-dependent reproduction. - J. Ecol., Oxford, 71:405-412.

Snell T. W. et Burch D. G. (1975): The effect of density on resource partitioning in *Chamaesyce hirta* (*Euphorbiaceae*). - Ecology, Durham, 56:742-746.

Solbrig O. T. et Simpson B. B. (1974): Components of regulation of a population of dandelions in Michigan. - J. Ecol., Oxford, 62: 473-486.

Solbrig O. T. et al. (1988): Studies on the population biology of the genus *Viola*. VI. The demography of *V. fimbriatula* and *V. lanceolata*. - J. Ecol., Oxford, 76:301-319.

Soukupová L. (1984): Changes in structure of vegetation on the old-fields in the Bohemian Karst. - Studie ČSAV, Praha, 18:1-15.

Sterk A. A. (1975): Demographic studies of *Anthyllis vulneraria* L. in the Netherlands. - Acta Bot. Neerl., Wageningen, 24:315-337.

Syrjanen K. et Lehtila K. (1993): The cost of reproduction in *Primula veris*: differences between two adjacent populations. - Oikos, Copenhagen, 67:465-472.

Towpasz K. et Szymska M. (1983) Structure and dynamics of populations of *Milium effusum* L. in a forest near Polanka-Haller in the Wielickie Foothills (Southern Poland). - Zesz. Nauk. UJ, Prace Bot., Kraków, 11:109-142.

Tutin T. G. et al. (1964-1980): Flora Europaea, Vol. 1-5. - Cambridge Univ. Press, Cambridge.

Ulrich B. (1984): Effect of air pollution on forest ecosystems and waters - the principles demonstrated at a case study in Central Europe. - Atmosph. Envir., London, 18:621-628.

Van Andel J. et Vera F. (1977): Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. - J. Ecol., Oxford, 65:747-758.

Zelená V. (1994): Předběžné shrnutí výsledků výzkumu pasečných společenstev Beskyd. - Zpravodaj Beskydy, „Vliv imisí na lesy a lesní hospodářství Beskyd", 6(1994):155-158, ed. LDF VŠZ Brno.

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