Folia Geobotanica 35: 403–417, 2000

PHRAGMITES AUSTRALIS AT AN EXTREME ALTITUDE: RHIZOME ARCHITECTURE AND ITS MODELLING

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Keywords: Architectural pattern of rhizomes, Common reed, High altitude, Spatially explicit model

Abstract: In central Europe *Phragmites australis* is a lowland plant, occurring rarely up to the tree line. In the Velká Kotlina cirque (Jeseníky mountains, NE Czech Republic), where it reaches its maximum altitude at about 1350 m a.s.l., its culms are 0.5–0.7 m high and the plants flower only in some years. During the last decade no germinable seeds have been observed. The architecture of *Phragmites* rhizomes from this site was studied on seven randomly selected clonal fragments. They consisted of 3 to 10 partial tussocks (clumps) and 4 to 17 green shoots. The total length of the rhizomes was 9.7 to 50 m per plant. The number of nodes per plant was 96 to 431 and the longest internodes were 83 mm long. The number of side branches was 31 to 105 per plant. The branching angle depended on the type of branched rhizome. The mean angles of horizontal rhizomes, which connect individual tussocks, were relatively wide (modus 45°, arithmetic mean 37°), whereas within a tussock much sharper angles of branching prevailed (modal value 5°, arithmetic mean 15°). The mean internode-to-internode angle on continuing rhizomes was about 8°, with a wide variation. An architectural, spatially-explicit model of *Phragmites* rhizome growth has been developed, showing that the *Phragmites* population in the studied locality can be maintained by vegetative multiplication, and seedling recruitment is not needed for its long-term persistence.

INTRODUCTION

Population dynamics of most plants in the northern temperate zone cannot be described without considering belowground structures, because nearly 70% of vascular plants are clonal (VAN GROENENDAEL & DE KROON 1990, KLIMEŠ et al. 1997) and shoots of most of them are inter-connected belowground. The growth and the spreading of clonal plants are linked with plant multiplication, and are largely determined in structures placed below the soil surface.

In many clonal plants the stems growing belowground form relatively simple two-dimensional structures. Their development can be described using a few growth rules (WALLER & STEINGRAEBER 1985, OBORNY & CAIN 1997). This simplicity stimulated the development of spatially-explicit individual-based models. Earlier deterministic models have largely been abandoned and replaced by stochastic models which are more realistic (WALLER & STEINGRAEBER 1985, CALLAGHAN et al. 1990). The aim of these models usually differs from those predicting biomass and carbon assimilation in plant stands. More emphasis is placed on the behaviour of individual ramets, plant spreading, spatial arrangement of the plant structures and on shoot-to-shoot interactions. In clonal plants which consist of repeated modules (usually defined as an internode with a node and attached roots, and eventually with a scale leaf which later decays; hereafter called segments), spatial arrangement of shoots belonging to individual clones is of great importance for population dynamics, because it determines the shape of the clone, its spreading, and especially interactions between shoots, and partly also the translocation of resources between shoots inter-connected by spacers. Real clones are usually large and complicated structures so that their parameters, such as displacement, ground area covered by them, shoot density, etc., cannot always be measured directly. Spatially explicit models may help, because by using parameters measured on clone fragments in the field, the models developed for a particular plant can be calibrated and long-term dynamics of clonal populations as well as larger scale patterns can be studied (KLIMEŠ 1992, COWIE et al. 1995, PIQUERAS & KLIMEŠ 1998, PIQUERAS et al. 1999).

This paper is focused on *Phragmites australis*, a plant which has been studied in detail during the last decades by numerous research teams. The biology of this grass is well known (RUDESCU et al. 1965, BJÖRK 1967, HASLAM 1972, VAN DER TOORN 1972, FIALA 1976). However, much attention has been paid to its aboveground organs – tall leafy culms bearing inflorescences. The role of belowground stems – rhizomes – has also been recognized, especially in studies focused on root ventilation and carbon storage and economy (ARMSTRONG & ARMSTRONG 1996, ARMSTRONG et al. 1996a,b, ČÍŽKOVÁ et al. 1996, KLIMEŠ et al. 1999). Nevertheless, the samples used for these studies were usually small, because it is difficult to dig out the extensive *Phragmites* rhizomes, penetrating to a considerable depth. Therefore, it is not surprising that available data on architectural patterns of the *Phragmites* rhizomes are poor and based on a relatively limited material.

I studied the rhizome structure of *Phragmites* at its maximum altitude at about 1350 m a.s.l. This particular locality was selected for two reasons. First of all, the occurrence of *Phragmites* at this altitude is interesting as the locality is in a glacial cirque and the *Phragmites* plants are accompanied by alpine plants, which is exceptional for this lowland species. Second, the extreme conditions, including shallow spring soils, made it possible to dig out entire clonal fragments (= physically inter-connected segments; hereafter referred to as clones) of *Phragmites*, which has never been done in the lowlands, as far as I know. To understand the long-term dynamics of *Phragmites*, a spatially explicit architectural model of *Phragmites* rhizome growth has been developed, based on growth rules describing the development of the rhizome structure. The model has been calibrated with the field data and used for studying the long-term dynamics, spreading and survival of *Phragmites* clones.

METHODS

Plant and locality

Phragmites australis (CAV.) TRIN. ex STEUD. (common reed) is a lowland plant forming monospecific or species-poor stands in the littoral zone of fishponds and lakes (HASLAM 1972). Exceptionally it may be found also in the mountains. For example, in the Alps it has been recorded at altitudes up to 1900 m a.s.l. (CONERT 1983). The plant is up to 4 m tall, with monocyclic shoots and long hypogeotropic rhizomes (SEREBRYAKOVA 1971, HASLAM 1972). The rhizomes are horizontal and vertical. Slant rhizomes develop rarely when the original growth direction of horizontal or vertical rhizomes is modified by physical obstacles, such as stones. Horizontally-growing rhizomes are initiated at the base of the mother shoot. Their growing tips bend up after a certain length of the horizontal rhizome is reached, which transforms into a short vertical rhizome later reaching the soil surface (HASLAM 1969a,b). Vertical rhizomes form annual leafy shoots without leaf rosettes. These are the mother shoots of new partial tussocks. The mother stem does not form a multiplication zone consisting of shortened internodes at its base, known from other monocyclic grasses (SEREBRYAKOVA 1971).

Shoots of the higher order making up the partial tussock are initiated along the whole vertical belowground stem. The partial tussock survives 3 to 6 years (HASLAM 1969b). During a single season stems of more than one order may be initiated. Moreover, higher-order stems are sometimes initiated on older parts of a partial tussock so that an estimation of the exact age of partial tussocks based on their morphology is often impossible (HASLAM 1972, KUDO & ITO 1988).

The maximum altitude of *Phragmites* in natural stands in the Czech Republic has been reported from the Velká and Malá Kotlina cirques (Jeseníky Mountains), where it occurs at altitudes of 1150 to 1350 m a.s.l. These records were reported first in 1843 (GRABOWSKI 1843), indicating that the species was not introduced to these localities recently. In *Phragmites* stands the water level in the Velká Kotlina cirque fluctuates during the vegetation season between about 10 cm above and 10 cm belowground level. *Phragmites* dominates there in several vegetation patches, up to a few hundred m^2 in size. It has colonized spring areas and narrow strips of wet meadow vegetation along streams, usually on peat soils. The total cover of vascular plants in *Phragmites* stands is 30–70% only, culms of *Phragmites* are 50–70 cm high. In the Velká Kotlina cirque *Phragmites* is usually accompanied by the following plants: *Molinia caerulea* (L.) MOENCH, *Deschampsia cespitosa* (L.) P. BEAUV, *Allium schoenoprasum* subsp. *sibiricum* (DC.) ČELAK., *Eriophorum angustifolium* HONCK. and *Trichophorum alpinum* (L.) PERS. The stand of *Phragmites* selected for this study was at 1350 m a.s.l., in a shallow depression filled with organic soil of about 20 cm deep, where *Phragmites* rhizomes cannot penetrate deeper due to firm bed-rock.

Field methods

Seven randomly selected clonal clones were carefully excavated in the locality in June, 1996. The samples were partly washed out in the field. Final washing of the rhizomes was carried out in the laboratory. Branching angles and angles between subsequent segments within a branch were measured in the field. Later, lengths of the numbered segments, rhizome diameter and culm height were measured.

Modelling of *Phragmites* rhizomes

Individual growth rules describe the growth of *Phragmites* only partially. The overall growth pattern is determined by their combination. Therefore, a simulation model based on the growth rules and calibrated with the field data has been developed to get a more complete picture of the rhizome growth of *Phragmites*. The growth of *Phragmites* plants was simulated in a homogeneous environment. Instead of biomass, I used the length of the segments as a measure of segment size. Similarly, field data were used for size-specific survival probabilities of ramets and branching angles.

In the simulations, a segment of *Phragmites* was placed in a homogeneous environment. Its growth was simulated in discrete units, plastochrons. A plastochron equals the time it takes for a segment along a branch to reach the same developmental stage as the last one (ERICKSON & MICHELINI 1957, BIRCH & HUTCHINGS 1992a). The relationship between plastochron and real time has not yet been studied in *Phragmites*, but the results based on other clonal plants have shown that there is a strong correlation between them. Moreover, for biological purposes the plastochron index is often a more efficient predictor of plant behaviour than the real time itself (ERICKSON & MICHELINI 1957, BIRCH & HUTCHINGS 1992b). An

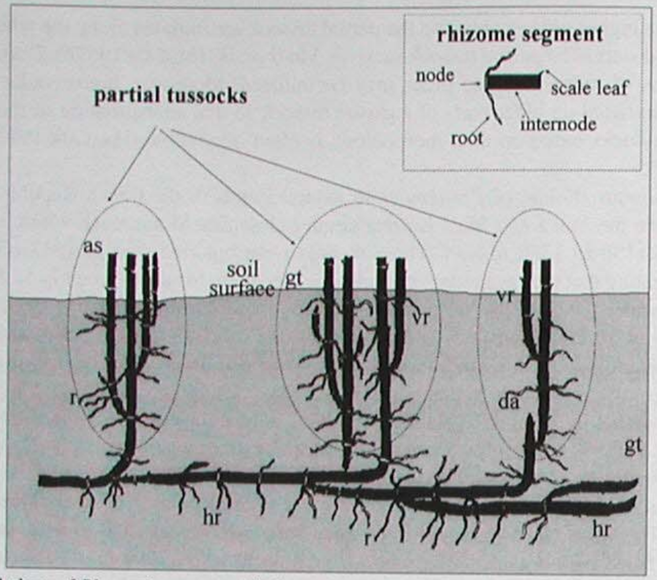

Fig. 1. Morphology of *Phragmites*. as – aerial shoot; r – root; hr – horizontal rhizome; vr – vertical rhizome; da – dead apex; gt – growing tip. Shoots aboveground are not shown.

important assumption in the simulation model was that the values of branching probabilities, branching angle and mortality operating in subsequent years were independent. In contrast, segment lengths within a branch were autocorrelated. Horizontal and vertical rhizomes of the plants were distinguished in the model and all variables and growth rules were considered separately for these two types of belowground stems. The growth of 300 independent clones was simulated for 1, 2, and 5, 10, 15, ..., 50 plastochrons. For technical details of the model see Appendix.

RESULTS

Rhizome morphology of *Phragmites*

As in many other perennial grasses the spatial pattern of *Phragmites* shoots is strongly aggregated due to the development of partial tussocks (Fig. 1). The studied clones consisted of 3 to 10 partial tussocks (Tab. 1). Out of these several older ones did not support any living shoot. The exact relative age of individual clones could not be estimated. However, the structure of the partial tussocks indicated a minimum age of about 7 years. The number of branches per clone was up to 105 but only 10 to 40% of them bore shoots with green leaves. The ratio between the number of green shoots in a year and the total number of shoots preserved in a clone was 2.6 to 9.5 for individual clones, which indicates that in the studied locality *Phragmites* rhizomes are preserved longer than in its typical stands in lowlands (e.g. VAN DER TOORN 1972, ČÍŽKOVÁ & LUKAVSKÁ 1999).

The morphology of horizontal and vertical rhizomes was markedly different. Branching was more frequent in vertical rhizomes than in horizontal ones (branching probability = 0.23 and 0.18, respectively; $P < 0.05$; for testing procedure see ZAR 1974: 284–286). Mother segment length strongly affected branching probability, both in horizontal and vertical rhizomes (Fig. 2A). Very short segments almost never branched, whereas the longest ones branched with a high probability, especially in horizontal rhizomes. Segment mortality was higher in vertical than in horizontal rhizomes (probability of mortality = 0.29 and 0.14, respectively; $P < 0.05$; for testing procedure see ZAR 1974: 284–286). The effect of segment size on its mortality was not as strong as for branching, and the mortality of the shortest segments of horizontal and vertical rhizomes was high and nearly equal (Fig. 2B). However, the mortality of the first five segments initiating side branches was on average only 0.05. In segments of about 2 mm long and longer, mortality was higher in vertical segments and for the longest segments it decreased in both rhizome types.

Table 1. Numbers of different structures in the clones studied in the Velká Kotlina cirque ($n = 7$).

	Average (s.d.)	Minimum	Maximum
Partial tussocks	5.4 (3.0)	3	10
Branches	57.0 (27.4)	31	105
Shoots bearing green leaves	10.1 (4.2)	4	17
Segments	209.1 (118.3)	110	421

Segments of horizontal rhizomes were longer than of the vertical rhizomes (14.2 and 5.8 mm on average, respectively; $t = 10.82$, d.f. = 1448, $P < 0.0001$; t-test). Very short segments strongly prevailed in vertical rhizomes. The frequency of horizontal segments of about 3 mm long and longer than 20 mm, however, was higher than that of vertical segments (Fig. 3). The maximum length of a segment was 83 mm. Segment length was autocorrelated within a branch. Subsequent segments usually had a similar length, both in the horizontal and vertical rhizomes. However, there was a tendency to produce slightly longer subsequent segments (Fig. 4). Besides the daughter segments which had their length comparable to that of the mother segments, very short segments were sometimes produced by longer mother segments both in horizontal and vertical rhizomes. These very short segments or their descendants usually died soon. It is likely that these unusual sequences of segment lengths were caused by rhizome injury.

Branches were nearly always initiated with a series of short segments. The first segment in a side branch was usually much longer in horizontal than on vertical rhizomes (0.95 and 0.56 mm, respectively; $P < 0.01$; t-test) and were rarely longer than 2 mm (Fig. 5). Due to this fact growth of the side branches was always much slower than that of the main rhizome.

The angle between the subsequent segments within a branch was usually smaller than 10° and angles wider than 30° were found rarely (Fig. 6A). The difference between the angles in horizontal and vertical rhizomes was poor, with slightly wider angles observed in horizontal rhizomes than on vertical rhizomes (9.9 and 7.0°, respectively; $P < 0.05$; t-test). However, there were great differences between the branching angles. Vertical rhizomes branched at very sharp angles, whereas in horizontal rhizomes angles below 20° were nearly missing and angles up to 90° were relatively frequent (Fig. 6B). Thus, the difference between the mean branching angles was strongly significant ($P < 0.0001$; t-test; the means were 15.2° and 52.2°, respectively).

The horizontal rhizomes were transformed into vertical ones always at about the same distance from the previous branching event, which indicates that a seasonal trigger could play a decisive role. The exact mechanism is still unknown. However, the first 8 ± 1 (mean ± s.d.)

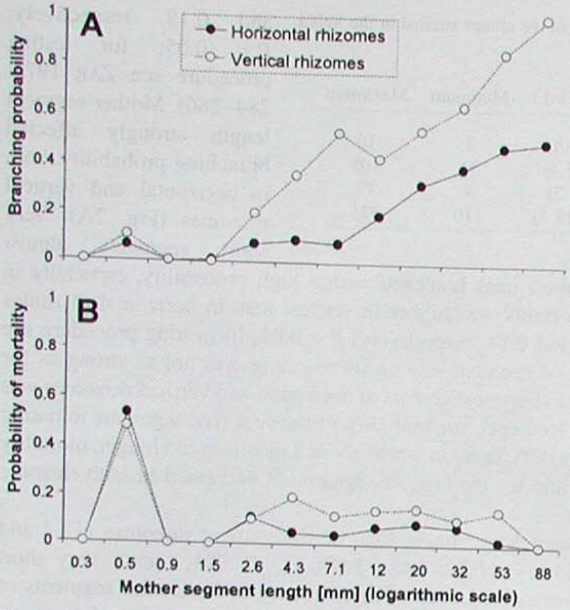

Fig. 2. The effect of mother segment length on branching (A) and mortality (B) in segments of horizontal and vertical rhizomes of *Phragmites*.

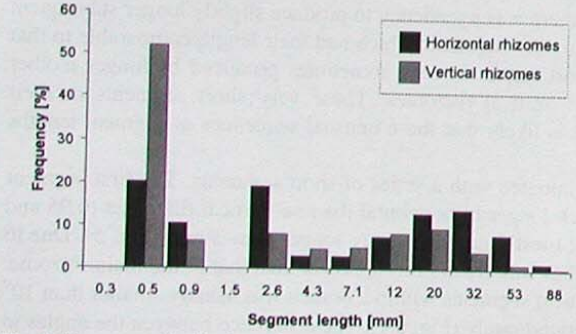

Fig. 3. Frequency distribution of segment lengths in horizontal and vertical rhizomes of *Phragmites*.

segments on a branch were nearly always horizontal and then the probability of rhizome bending and transformation into a vertical rhizome became about 0.5. As no more than one partial turf is usually established on a horizontal rhizome during one growing season in the studied locality (pers. observ.), 8 plastochrons on horizontal rhizomes correspond to one year, at the most.

The length of the vertical rhizomes was limited by the depth at which horizontal rhizomes grew. On average 12.5 ± 2.1 (mean ± s.d.) segments were produced on vertical stems before the soil surface was reached.

Simulation results

The shape and spatial structure of the simulated clones resembled the real ones (Fig. 7). The mortality of *Phragmites* was very high at the beginning of clone growth. After the first 20 plastochrons only 50% of the plants were still alive and about one-third of the plants survived until plastochron 50 (Fig. 8). However, the mean number of segments – both horizontal and vertical – produced at each plastochron markedly increased in time (Fig. 9).

The mean age of simulated clones at a plastochron increased with the plastochron index but the relationship was curvilinear (Fig. 10A) due to clone mortality. However, the mean area covered by a living clone (defined as the smallest convex polygon including all segments) increased rapidly (Fig. 10B). The sum of segment lengths increased in a similar fashion (Fig. 10C). In contrast, the clone displacement, defined as the longest distance between the initial segment and any other segment belonging to the same clone, increased steadily but the increase slowed down in time (Fig. 10D). Finally, the clone perimeter increased linearly during the first 50 plastochrons (Fig. 10F).

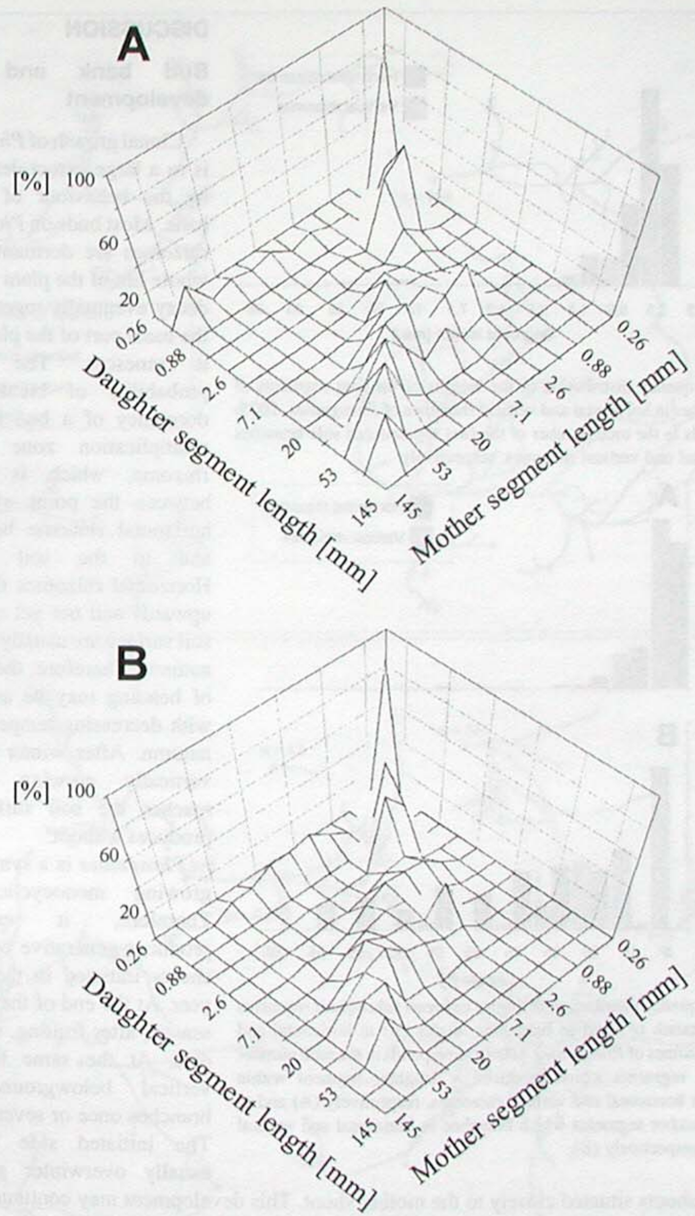

Fig. 4. Frequencies of transitions between size categories from mother to next daughter segments. The segments were measured on horizontal (A) and vertical (B) rhizomes of *Phragmites*. 100% corresponds to the total number of mother segments which produced a daughter segment in horizontal (A) and vertical (B) rhizomes.

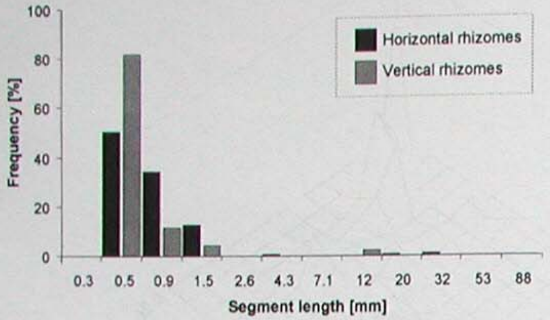

Fig. 5. Frequency distribution of the lengths of the first segments of side branches in horizontal and vertical rhizomes of *Phragmites*. 100% corresponds to the total number of the first segments of side branches in horizontal and vertical rhizomes, respectively.

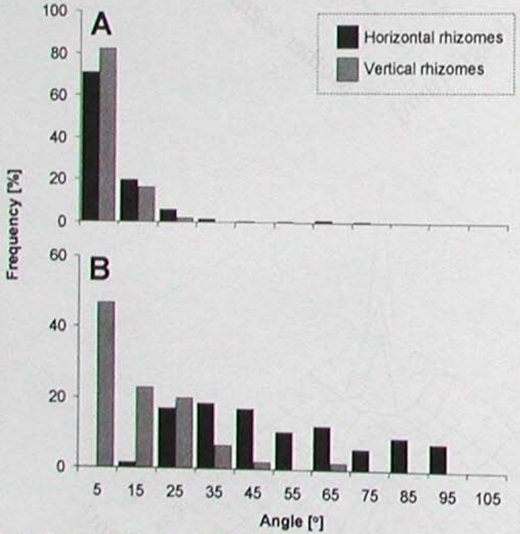

Fig. 6. Frequency distribution of angles between subsequent segments within a branch (A) and of branching angles (B) in horizontal and vertical rhizomes of *Phragmites*. 100% corresponds to the total number of mother segments which produced a daughter segment within a branch in horizontal and vertical rhizomes, respectively (A) and to the total number segments which branched in horizontal and vertical rhizomes, respectively (B).

DISCUSSION

Bud bank and plant development

Clonal growth of *Phragmites* is to a large extent determined by the behaviour of its bud bank. Most buds on *Phragmites* rhizomes are dormant for the whole life of the plant and they decay eventually together with the basal part of the plant when it senesces. The highest probability of breaking the dormancy of a bud is at the multiplication zone of the rhizome, which is situated between the point where the horizontal rhizome bends up, and to the soil surface. Horizontal rhizomes that bend upwards and not yet reach the soil surface are usually found in autumn. Therefore, the process of bending may be associated with decreasing temperature in autumn. After winter rest, the vertically growing rhizome reaches the soil surface and produces a shoot.

Phragmites is a sympodially growing monocyclic plant. Therefore, it eventually produces generative organs on shoots initiated in the current year. At the end of the growing season, after fruiting, the shoot dies. At the same time, the vertical belowground stem branches once or several times. The initiated side branches usually overwinter and then produce shoots situated closely to the mother shoot. This development may continue for 3 to 6 years (Haslam 1969b), rarely longer (this study). The partial tussock formed in this way consists of several vertical rhizomes of different ages. After the partial tussock dies, it can be (partly) preserved and remain attached to the still-living horizontal rhizome.

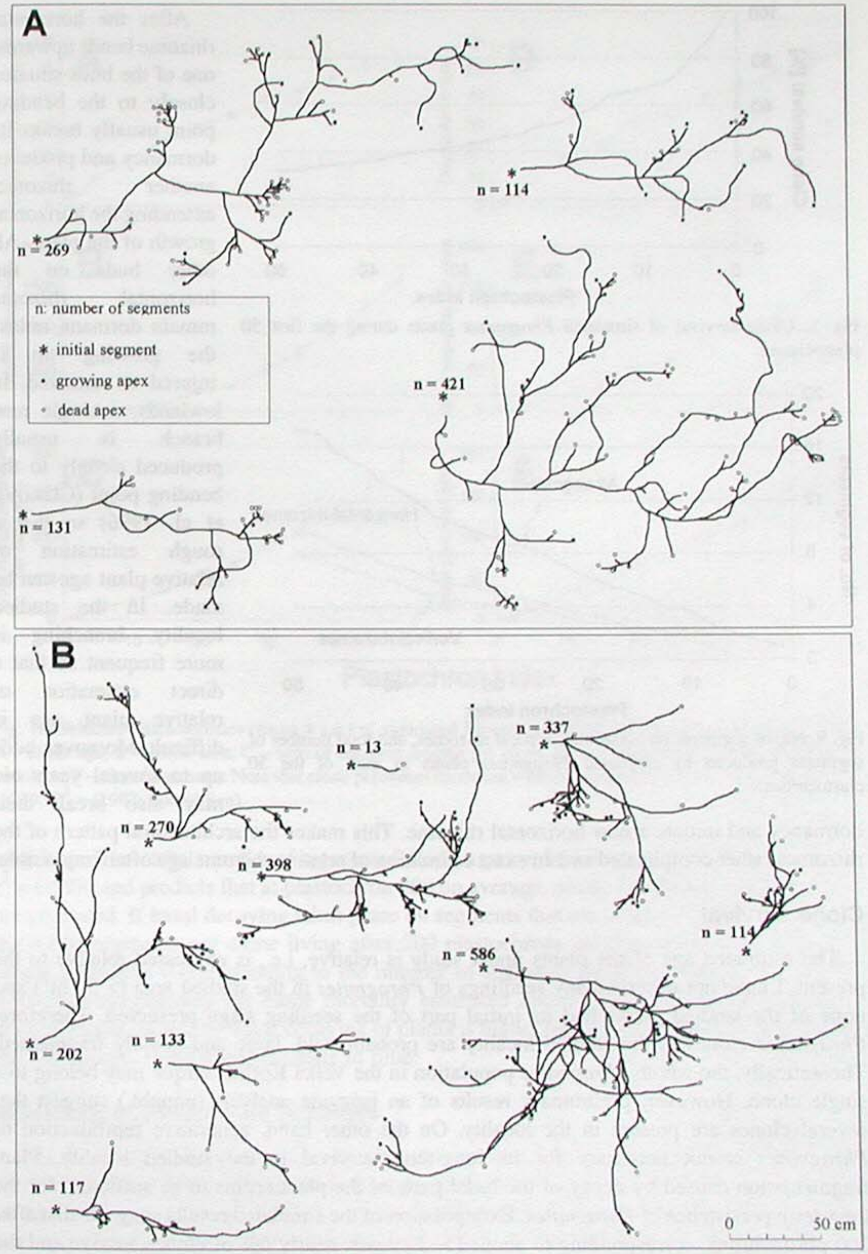

Fig. 7. Examples of rhizome architecture of *Phragmites* based on real plants studied in the field (A) and simulated clones run for 50 plastochrons (B). Segment is the node and attached internode.

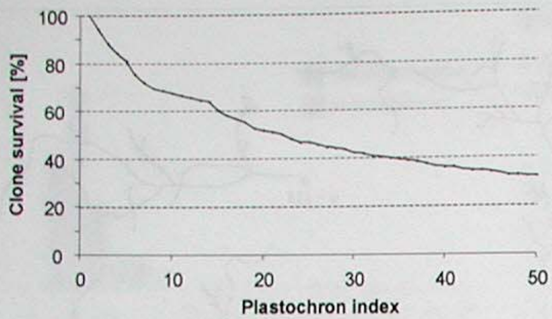

Fig. 8. Clone survival of simulated *Phragmites* plants during the first 50 plastochrons.

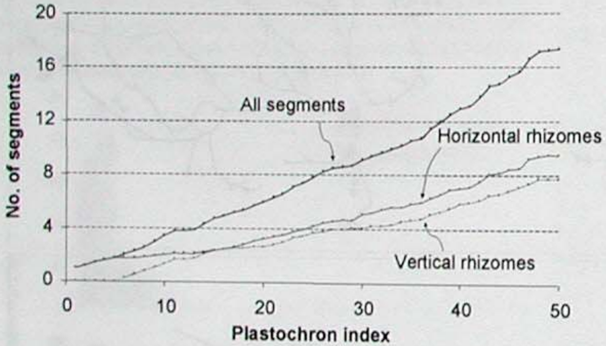

Fig. 9. No. of segments on horizontal, vertical rhizomes, and total number of segments produced by simulated *Phragmites* plants in each of the 50 plastochrons.

After the horizontal rhizome bends upwards, one of the buds situated closely to the bending point usually breaks its dormancy and produces another rhizome, extending the horizontal growth of the plant. All other buds on the horizontal rhizome remain dormant, unless the growing tip is injured or removed. In lowlands, a single new branch is usually produced closely to the bending point (Čížková et al. 1996) so that a rough estimation of relative plant age can be made. In the studied locality, branching is more frequent so that a direct estimation of relative plant age is difficult. Moreover, buds up to several years old may also break their dormancy and initiate a new horizontal rhizome. This makes the architectural pattern of the rhizomes rather complicated and an exact estimation of relative rhizome age often impossible.

Clone survival

The estimated age of the plants under study is relative, i.e., is expressed relative to the present. I have not observed any seedlings of *Phragmites* in the studied area (> 50 m^2) and none of the studied plants had its initial part of the seedling stage preserved. Therefore, *Phragmites* clones in the studied locality are probably old, large and heavily fragmented. Theoretically, the whole *Phragmites* population in the Velká Kotlina cirque may belong to a single clone. However, preliminary results of an isozyme analysis (unpubl.) suggest that several clones are present in the locality. On the other hand, generative reproduction of *Phragmites* is not necessary for its long-term survival in the studied locality. Plant fragmentation caused by decay of the basal parts of the plant seems to be sufficient for the long-term persistence of *Phragmites*. Extrapolation of the simulated results suggests that after 200 plastochrons, corresponding to about 15–25 years, nearly 6% of clones survive and the last clone of the 300 simulated ones is expected to die after 266 plastochrons (Fig. 8; no. of surviving clones = $-59.3 * \ln(\text{plastochron}) + 331.2$; $r^2 = 0.982$). The last surviving clones are very large. Their total number of segments follows a power function ($y = 9.9 * \text{plastochron}^{1.32}$; $r^2 = 0.999$) and predicts that at plastochron 200 on average, nearly 11,000 segments per clone are produced. If basal decaying takes place on segments that are at least 40 plastochrons old, the 4,850 segments per clone living after 200 plastochrons are fragmented into about 100 clonal fragments (corresponding to the number of segments produced at plastochron 160). This over-compensates the clone mortality estimated above. Therefore, in the long term, multiplication caused by basal decaying of plants is higher than clone mortality, and therefore the *Phragmites* population increases in time.

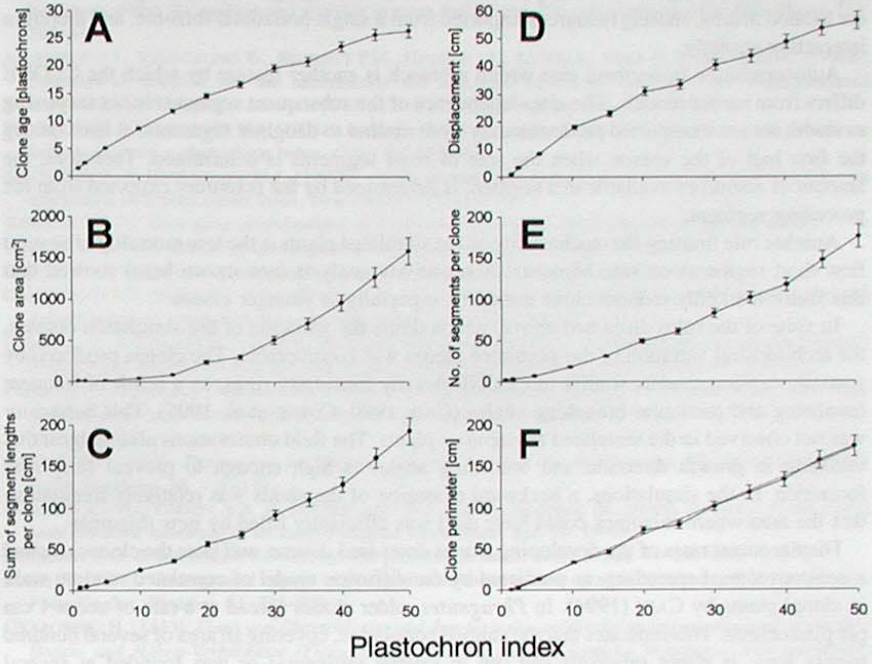

Fig. 10. Selected characteristics (mean ± s.e.) of simulated *Phragmites* plants during the first 50 plastochrons. A – clone age, B – clone area, C – sum of segment lengths per clone, D – displacement, E – no. of segments per clone, F – clone perimeter. Note that clone perimeter increased with the plastochron index linearly ($y = 3.55x - 4.39$, $R^2 = 0.997$; dotted line).

Modelling of *Phragmites* rhizomes

The model presented here is an extension of the previously developed version of the model CLONE (Klimeš 1992, Piqueras & Klimeš 1998, Piqueras et al. 1999). The new version of CLONE is one of the few spatially-explicit models which combines two types of rhizomes. In contrast to most other models of clonal plants (e.g. Cain 1990, Klimeš 1992, Cowie et al. 1995, Adachi et al. 1996), it has been specifically adjusted to a grass and includes the specific rhizome growth within partial tussocks. The role of partial tussocks should not be neglected in grasses nor in many other clonal plants as the shoots belonging to individual partial tussocks are located nearby, sharing resources imported from a single horizontal rhizome, and therefore interacting strongly.

Autocorrelation in segment size within a branch is another feature by which the CLONE differs from earlier models. The size-dependence of the subsequent segments is not surprising as resources are transported predominantly from mother to daughter segments, at least during the first half of the season when the size of most segments is determined. Therefore, the amount of resources available in a segment is determined by the resources exported from the preceding segment.

Another rule limiting the stochasticity of the simulated plants is the low mortality of several first short segments on side branches. A sensitivity analysis (not shown here) showed that this factor markedly reduces clone mortality, especially in younger clones.

In spite of the rules discussed above, which limits the variation of the simulation outputs, the architectural variation of the simulated clones was considerable. The clones produced by spatially-explicit models similar to CLONE usually form fairy rings, as a result of frequent branching and particular branching angles (Cain 1990, Cowie et al. 1995). This behaviour was not observed in the simulated *Phragmites* plants. The field observations also suggest that variation in growth direction and branching angles is high enough to prevent fairy ring formation. In the simulations, a backward extension of the plants was relatively frequent so that the area where rhizomes could have died was efficiently filled by new rhizomes.

Displacement rates of the developing clones decreased in time, and later the clones reached a constant rate of spreading, as predicted by the diffusion model of correlated random walk in clonal plants by Cain (1994). In *Phragmites*, older clones spread at a rate of about 1 cm per plastochron. This indicates that the studied population, covering an area of several hundred meters long, is either relatively old (up to several millennia) or was founded at several microlocalities. According to literature *Phragmites*, is known from the Velká Kotlina cirque from the middle of the last century (Grabowski 1843, Jeník et al. 1983). However, *Phragmites* could occasionally have been introduced by humans even earlier because the grasslands in the Velká Kotlina cirque were mown already in the 18th century and the hay was transported to neighbouring villages at the foot of the mountains (Hošek 1973, Klimeš & Klimešová 1991) where several larger localities of *Phragmites* still exist. Therefore, also a relatively recent introduction of *Phragmites* to the Velká Kotlina cirque by human activities cannot be excluded.

Acknowledgements: This work was financially supported by grant 206/95/0508 of the Grant Agency of the Czech Republic and by grant no. M44 of the Agency for Nature Conservation and Landscape Protection of the Czech Republic (a part of the programme "Care of the environment" of the Ministry of environmental protection no. 6110/2). The English was improved by J.W. Jongepier. I thank Karen Kotschy and three anonymous reviewers for constructive comments, J. Klimešová for the drawing of common reed and B. Kučerová for technical assistance.

REFERENCES

Adachi N., Terashima I. & Takahashi M. (1996): Mechanisms of central die-back of *Reynoutria japonica* in the volcanic desert on Mt Fuji. A stochastic model analysis of rhizome growth. *Ann. Bot. (Oxford)* 78: 169–179.

Armstrong J. & Armstrong W. (1996): A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. ex Steud. *Aquatic Bot.* 39: 75–88.

Armstrong J., Armstrong W. & van der Putten W.H. (1996a): *Phragmites* die-back: Bud and root death, blockages within the aeration and vascular systems and the possible role of phytotoxins. *New Phytol.* 133: 399–414.

Armstrong J., Armstrong W., Beckett P.M., Halder J.E., Lythe S., Holt R. & Sinclair A. (1996b): Pathways of aeration and the mechanisms and beneficial effects of humidity- and Venturi-induced convections in *Phragmites australis* (Cav.) Trin. ex Steud. *Aquatic Bot.* 54: 177–197.

Birch C.P.D. & Hutchings M.J. (1992a): Analysis of ramet development in the stoloniferous herb *Glechoma hederacea* using a plastochron index. *Oikos* 63: 387–394.

Birch C.P.D. & Hutchings M.J. (1992b): Stolon growth and branching in *Glechoma hederacea* L.: an application of a plastochron index. *New Phytol.* 122: 545–551.

Björk S. (1967): Ecological investigations of *Phragmites communis*. *Folia Limnol. Scand.* 14: 3–248.

Cain M. L. (1990): Models of clonal growth in *Solidago altissima*. *J. Ecol.* 78: 27–46.

Cain M. L. (1994): Consequences of foraging in clonal plant species. *Ecology* 75: 933–944.

Callaghan T.V., Svensson B.M., Bowman H., Lindley D.K. & Carlsson B.Å. (1990): Models of clonal growth based on population dynamics and architecture. *Oikos* 57: 257–269.

Čížková H. & Lukavská J. (1999): Rhizome age structure of three populations of *Phragmites australis* (Cav.) Trin. ex Steud.: biomass and mineral nutrient concentrations. *Folia Geobot.* 34: 209–220.

Čížková H., Lukavská J., Přibáň K., Kopecký J. & Brabcová H. (1996): Carbohydrate levels in rhizomes of *Phragmites australis* at an oligotrophic and a eutrophic site: A preliminary study. *Folia Geobot. Phytotax.* 31: 111–118.

Conert H.J. (1983): *Phragmites*. In: Hegi G., *Illustrierte Flora von Mitteleuropa, I/3*, Verlag Paul Parey, Berlin-Hamburg, pp. 126–139.

Cowie N.R., Watkinson A.R. & Sutherland W.J. (1995): Modeling the growth dynamics of the clonal herb *Anemone nemorosa* in an ancient coppice wood. *Abstr. Bot.* 19: 35–49.

Erickson R.O. & Michelini F.J. (1957): The plastochron index. *Amer. J. Bot.* 44: 297–305.

Fiala K. (1976): Underground organs of *Phragmites communis*, their growth, biomass and net production. *Folia Geobot. Phytotax.* 11: 225–259.

Grabowski H. (1843): *Flora von Oberschlesien und dem Gesenke, mit Berücksichtigung der geognostischen, Boden- und Höhen-Verhältnisse (Flora of Upper Silesia and the Jeseníky Mountains, with geognostic, pedological, and altitudinal results)*. Breslau.

Haslam S.M. (1969a): Stem types of *Phragmites communis* Trin. *Ann. Bot. (Oxford)* 33: 127–131.

Haslam S. M. (1969b): The development and emergence of buds in *Phragmites communis* Trin. *Ann. Bot. (Oxford)* 33: 289–301.

Haslam S. M. (1972): *Phragmites communis* Trin. *J. Ecol.* 60: 585–610.

Hošek E. (1973): Vývoj dosavadního hospodaření v nejvyšších polohách Jeseníků a jeho vliv na horní hranici lesa (The development of the past management at the highest altitudes of the Jeseníky Mountains, and its effect on the tree line). *Campanula* 4: 69–81.

Jeník J., Bureš L. & Burešová Z. (1983): Revised flora of Velká Kotlina cirque, the Sudeten Mountains. *Preslia* 55: 25–61.

Klimeš L. (1992): The clone architecture of *Rumex alpinus* (*Polygonaceae*). *Oikos* 63: 402–409.

Klimeš L. & Klimešová J. (1991): Alpine tundra in the Hrubý Jeseník Mts., the Sudeten, and its tentative development in the 20th century. *Preslia* 63: 245–268.

Klimeš L., Klimešová J. & Čížková H. (1999): Carbohydrate storage in rhizomes of *Phragmites australis* (Cav.) Trin. ex Steud.: the effects of altitude and rhizome age. *Aquatic Bot.* 64: 105–110.

Klimeš L., Klimešová J., Hendriks R. & van Groenendael J. (1997): Clonal plant architectures: a comparative analysis of form and function. In: de Kroon H. & van Groenendael J. (eds.), *The ecology and evolution of clonal plants*, Backhuys Publishers, Leiden, pp. 1–29.

Kudo G. & Ito K. (1988): Rhizome development of *Phragmites australis* in a reed community. *Ecol. Res. (Tokyo)* 3: 239–252.

Oborny B. & Cain M.I. (1997): Models of spatial spread and foraging in clonal plants In: de Kroon H. & van Groenendael J. (eds.), *The ecology and evolution of clonal plants*, Backhuys Publishers, Leiden, pp. 155–183.

Piqueras J. & Klimeš L. (1998): Clonal growth and population dynamics in the pseudoannual plant *Trientalis europaea* L. *Pl. Ecol.* 136: 213–227.

PIQUERAS J., KLIMEŠ L. & REDBO-TORSTENSSON P. (1999): Foraging in the clonal plant *Trientalis europaea* L.: Modelling of the morphological response to nutrient availability. *Pl. Ecol.* 141: 117–127.

RUDESCU L., NICULESCU C. & CHIVU I.P. (1965): *Monografia stufului din Delta Dunârii* (*A monograph of the Donau Delta*). Editura Academii Republicii Socialiste Romania, Bucureşti.

SEREBRYAKOVA T. I. (1971): *Morfogenez pobegov i evolyutsiya zhiznennykh form zlakov* (*Morphology of tillers and evolution of life-forms of grasses*). Nauka, Moskva.

VAN DER TOORN J. (1972): *Variability of* Phragmites australis *(CAV.) TRIN. ex STEUDEL.* 's-Gravenhage.

VAN GROENENDAEL J. & DE KROON H. (1990): Preface. In: VAN GROENENDAEL J. & DE KROON H. (eds.), *Clonal growth in plants: regulation and function.* SPB, The Hague, pp. vii-ix.

WALLER D.M. & STEINGRAEBER D.A. (1985): Branching and modular growth: Theoretical models and empirical patterns. In: JACKSON J., BUSS L. & COOK R. (eds.), *Population biology and evolution of clonal organisms*, Yale University Press, New Haven, pp. 225–257.

ZAR J. (1974): *Biostatistical analysis.* Prentice Hall, Inc., Engelwood Cliffs.

Received 26 July 1999, revison received 11 January 2000, accepted 10 August 2000
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APPENDIX

Details of the simulation model

For simulations the stochastic spatially explicit model CLONE (see above) was used, which was adapted to include peculiarities of the growth of *Phragmites* rhizomes. The major change in the current version of CLONE in comparison with older versions is that horizontal and vertical rhizomes behave according to different rules. The program is an MS-DOS application written in Turbo Pascal. It produces both text and graphic output, and consists of 3,750 lines of code. To get simulated plants resembling those studied in the field I calibrated the simulation model by the field data. Individual clones are simulated independently of each other and no interaction between rhizomes or shoots within a clone is included. The simulation of a plant starts with a single segment, which is placed into a homogeneous environment. No ontogenetic changes of growth rules are included into the model so that, for example, branching probability of a segment with a given length is always the same, no matter whether the whole clone consists of one or a thousand segments. During a time unit which equals to one plastochron, several decisions are being made in the following order. Will the segment survive until the text time? If the answer is yes, then: what will be the angle between the mother segment (formed at time t) and its daughter segment (formed at time t+1), what will be the length of the daughter segment, will the mother segment branch? If the answer to the last question is yes, then: what will be the branching angle, what will be the length of the first segment on the side branch?

In a simulation each segment has its number and 22 other variables which include segment co-ordinates, segment predecessor and successors (i.e. daughter segments) each coded with a number, segment type (horizontal or vertical), segment status (living or dead), its relative age within a branch in plastochrons, and several other, more technical variables.

The simulation is stochastic, i.e. individually simulated plants usually differ from each other, even if the same growth rules were used to simulate them. However, the dependence of length of daughter segment on the length of mother segment limits the stochasticity considerably. Segment length was not taken randomly from its observed frequency distribution. Instead, individual frequency distributions were calculated for different classes of mother segment length. Simulation stochasticity was further reduced by using a specific frequency distribution for the length of the first segments on side branches. Moreover, no mortality of these short segments nor that of up to five subsequent segments has been observed in the field (presumably due to the support from the older parts of the rhizome).

Growth rules

1. Size of the first segment in a simulation was taken from the observed distribution of segment sizes in horizontal rhizomes (Fig. 3).
2. Branching probability was segment-size dependent and differed between horizontal and vertical rhizomes (Fig. 2A).
3. Mortality was treated in the same way as branching probability (Fig. 2B), except for the mortality of the first 5 segments on side branches which was set to zero.
4. The probability of transformation of horizontal into vertical rhizomes in the first 7 segments on horizontal branches equals to zero, in subsequent segments (i.e., for segments preceded by at least 7 horizontal segments which did not produce vertical segments) it equals to 0.5.
5. The length of daughter segments (except for the first segment on side branches) was taken from frequency distributions calculated for individual classes of mother segment lengths, for horizontal and vertical rhizomes apart (Fig. 4A and B).
6. The length of the first segment on side branches was taken from Fig. 5, for horizontal and vertical rhizomes apart.
7. Angles between subsequent segments within a branch were taken from Fig. 6A, for horizontal and vertical rhizomes apart.
8. Branching angles were taken from Fig. 6B, for horizontal and vertical rhizomes apart.
9. Vertical rhizomes reached the soil surface and formed shoots with a probability of 0.8, after 12 segments had been developed on individual vertical rhizomes.