

## On the growth form of bog pine, *Pinus x pseudopumilio*

### O růstové formě blatkové kleče (*Pinus x pseudopumilio*)

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#### Abstract

The growth form of *Pinus x pseudopumilio* (Willk.) Beck, a stabilized hybrid in Rokytecká Bog in the montane zone of Bohemian Forest, develops according to Rauh's architectural model. Duration of the model-conform period and structural details vary due to the age, environmental factors and, presumably, genetic variation. Early loss of dominance of the apical meristem in sapling's primary axis is followed by enhanced acrotonic branching in several limbs whose distal orthotropic sections are expanded by rhythmic/annual growth of "primary proleptic branches" and create the ultimate sabre-shaped skeleton of the mature "krummholz". On older twigs, limbs and boles, in the area of "rings" created by clustered bud-scale scars, the accessory buds revive or arise *de novo*, and produce "secondary proleptic branches". Their frequency throughout the analyzed stand did not show significant relationships to general pattern of the studied mire, but most of the secondary branches remained needle-poor and stunted over several decades, thus exerting little effect on the growth form of individual plants. The number of the leafy internodes varied between 3 and 9 and was not significantly lower towards the centre of the mire.

*Key words:* krummholz, architectural model, secondary branch, ombrotrophic mire, Bohemian Forest

#### Site and taxon under study

Our short contribution to the knowledge of the growth form of bog pine refers to the extensive peatlands of Rokytecká sláť (hereafter Rokytecká Bog) situated at about 49°05'N, 13°25'E, and 1100 a.s.l., to the east of Rachel/Roklan (1453 m a.s.l.), a prominent massif of Bohemian Forest and topmost summit of the Bavarian Forest National Park. In terms of SOUKUPOVÁ (1996) the mires of Rokytecká Bog belong to a complex of the prevailingly nutrient-poor, ombrotrophic vegetation of the *Oxycocco-Sphagnetea*, a phytosociological rank governed by *Sphagnum* mosses, ericaceous shrubs and non-arboreal pine populations possessing several procumbent "trunks" reaching a height of up to 6 m. According to Skalický (in SKALICKÁ 1988) these "fruticose" pines are taxonomically identified as *Pinus x pseudopumilio* (Willk.) Beck, and represent a product of widespread introgressive hybridisation between the fruticose *Pinus mugo* Turra (borovice kleč in Czech) and arboreal *Pinus rotundata* Link (borovice blatka in Czech), the two coniferous taxa growing in Bohemian Forest, respectively, on the rocks (summits, scree and glacial corries), and on mires of lower altitude. On the nearby mires of the Austrian territory, STEINER (1992) calls the single-stem tree as *Pinus uncinata* Mill. ex. Mirb. *s.str.*, and the non-arboreal krummholz as *Pinus rotundata* Link.

According to Flora Europaea (TUTIN 1993) the respective arboreal pine is classed as *Pinus uncinata* Mill. ex Mirb., and the non-arboreal taxon is treated merely as intraspecific variety *Pinus uncinata* var. *rotundata*. In the absence of modern taxonomical treatment of this pine complex, we use the above mentioned classification of Skalický, and propose the common names “krummholz pine” and “blatková kleč” as the English and Czech equivalents for *Pinus x pseudopumilio*.

### Terminology of non-arboreal pines

Description of the growth forms in woody plants is still far from a desirable unification. Classical morphological approach, such as summarised by DOSTAL & FUTÁK (1966), is no more applicable in the case of clear distinction between arboreal and fruticose species. This refers also to the pines. While describing the unlimited growth form of multistemmed pines interconnected by adventitious rooting in a study on *Pinus mugo* in the Giant Mountains, ŠTURSA (1966) used the term “polycormon”. OLDEMAN (1990:110–113) summarised the issue of the architecture of shrubs, and proposed a tentative pattern, stressing the alternating basitonic and acrotonic branching. Currently, the habit of the widespread non-arboreal *Pinus mugo* in mountains is frequently resolved by the generalised concept of “krummholz”, a term derived from German, but inconsistently used in English for any stunted form of trees found above the timberline (ART 1993).

As explained by KAENNEL & SCHWEINGRUBER (1995: 198–199) the concept of “krummholz” refers to two different growth forms: (1) woody plants with genetically curved, prostrate stems, and (2) stunted, crippled trees which grow on mechanically stressed sites. The former definition matches the growth form of *Pinus x pseudopumilio* on mires in Bohemian Forest. In the development of its krummholz habit, obviously, both the basitonic and the acrotonic branching pattern combine.

A further step in the “architectural analysis” of *Pinus x pseudopumilio* requires the application of the terminology proposed by HALLÉ & al. (1978). According to their morphogenetical distinction of two contrasted types of lateral branches (sylleptic branches versus proleptic branches) the Rauh’s model in temperate pines is necessarily dominated by „primary“ proleptic branches which rhythmically develop from terminal meristems after the period of rest in winter. In terms of OLDEMAN (1990) proleptic axes are “organs lying in wait for hormonal signals from inside the tree or outside environment”. Obviously the lateral branches developed occasionally on trunks, limbs and twigs of the krummholz pine “out of sequence of annual branching” are a product of similar response to internal or external factors (air pollution is a suspected factor in the studied area). They develop from „secondary bud complex“ (sensu HALLÉ & al. 1978) and thus can be called „secondary proleptic branches“, shortly „secondary branches“. The same organs are called by dendrologists and foresters by other terms: accessory shoots, epicormic shoots, stem suckers and even sprouts.

### Branching system

In the studied Rokytecká Bog, stands of the non-arboreal/multistemmed *Pinus x pseudopumilio* consist of separate individual plants which result from basitonic branching at/below ground level, and develop, on the average, 3 to 5 prominent “skeleton” limbs with typical acrotonic branching. While the proximal section of the limb is prostrate and sabre-shaped, its distal section grows in upright direction, reaching a uniform height of several meters, controlled by environmental factors. The procumbent proximal sections tend to be successively covered by mosses and *Vaccinium uliginosum* and later buried by peat accretion. Inside the

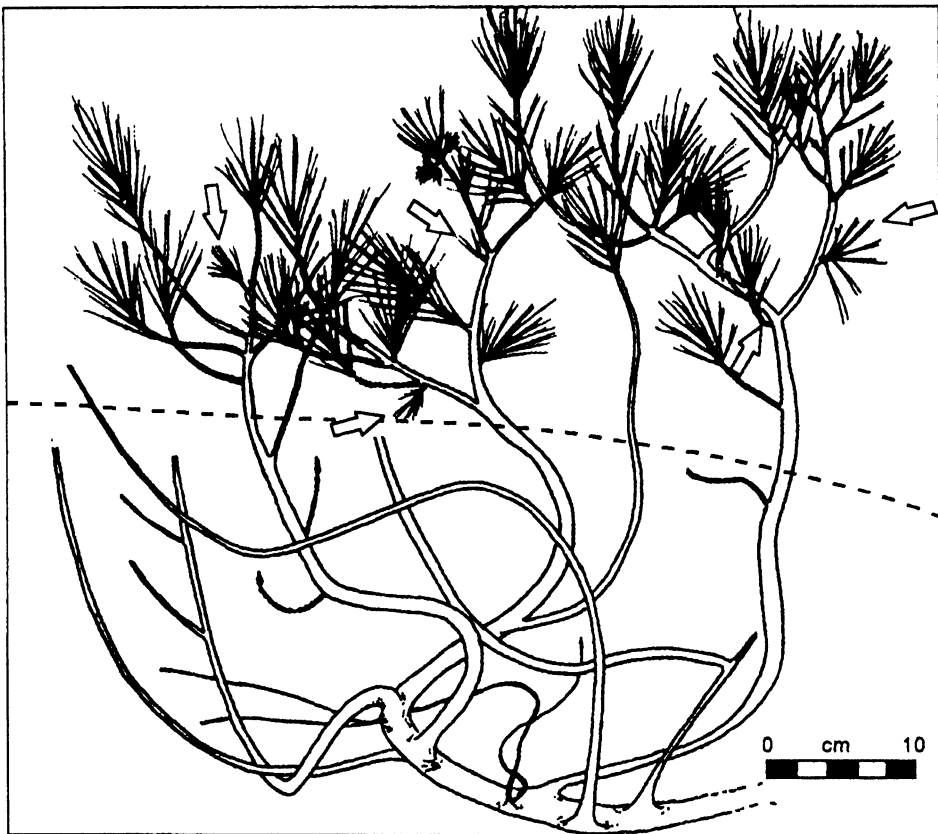


Fig. 1. – Young krummholz of *Pinus x pseudopumilio* developed inside and above a mound of bryophytes on Rokytecká Bog in Bohemian Forest; dashed line marks the surface of the mound; the arrows indicate secondary branches.

thick stands of krummholz pine, the surface peat layer contains a tangle of both live and half-rotten trunks. The near-the-ground limbs of *Pinus x pseudopumilio* serve as natural scaffolding promoting the upward growth of *Sphagnum magellanicum* and ericaceous shrublets, thus enhancing the natural elevation of the surface of ombrotrophic mires. Fig. 1 shows the coexistence of the skeleton limbs of a young krummholz pine specimen and associated bryophytes, mainly *Sphagnum magellanicum*, forming an elevated layer of acrotelm. In the stands of Rokytecká Bog, the oldest skeleton limbs surpass the age of 100 years and attain 20 to 25 cm in diameter at their proximal part, and reach 6 m in height. Adventitious roots appear in *Pinus x pseudopumilio* near the scaped periderm on the sabre-shaped basis of the limbs, but they seem to be less frequent than in *Pinus mugo* populations studied by ŠTURSA (1966) in the Giant mountains. Remarkably, in an excavated young specimen, adventitious roots branched even from the upper side of a horizontal limb.

The distal part of the skeleton trunks in *Pinus x pseudopumilio* conforms with the Rauh's model (HALLÉ & al. 1978), but individual pine specimens in various localities of Bohemian Forest display a considerable diversity in size and age structure, in annual longitudinal and

radial increments, frequency of branching, duration of needles, and structure of cones. As suggested by Skalický (in SKALICKÁ 1988), these differences can be explained by gene recombination and hybridisation taking place during the period of Postglacial when the fruticose *Pinus mugo* and arboreal *P. rotundata* were more frequent and situated closer to each other in mountains of Central Europe. Beside this genetic variation, numerous environmental factors affected the details of general growth forms and their distribution in closed stands. Position within the mire complex appears most effective: marginal zone (lagg) with shallow peat, better drainage, accessible mineral soil and competition of the associated Norway spruce decide on the outer limits of krummholz pine stands. Branching and “fruiting” of the terminal shoots and duration of needles are predictably affected by ground water, snow pressure, exposure to sun, wind action and, possibly, air pollution. Fluctuation of the ground water in Rokytecká Bog in 1997 and 1998 showed the highest water level in the bog centre, followed by the outer margin of the bog (lagg), and the lowest water level on the transition towards the bog centre; however, the growth habit of the krummholz pine cannot be easily explained in terms of ground water level.

Besides some general morphological observations we performed a tentative study of the status of the krummholz pine along eight transects 100 m in length, situated between the top-most bog centre and northern lagg of Rokytecká Bog, at 1120 m a.s.l. The eight parallel transects ran at 20 m distance from each other. Along the transect at every 5 m interval a dominant shoot (skeleton limb) reaching the canopy has been selected for the assessment of the needle-bearing internodes and occurrence of the accessory (secondary proleptic) branches.

For the statistical evaluation of collected data sets the nonparametric Kruskal-Wallis test was applied. No significant difference was found among the eight transects, which suggested that all data from these transects were appropriate for the following analyses. The data from each interval from all transects were afterwards compared (again by Kruskal-Wallis test at  $p=0.001$ ). Significant differences were consistently found for the needle-bearing internodes between the intervals of 0 to 15 m and the rest of the transects; therefore the grouped segments (0 to 15 m and the rest) were tested by means of ANOVA. Number of secondary proleptic branches showed broad variability, any significant differences were distinguished neither for individual transect intervals nor for the grouped segments of the transects.

### **Rauh's architectural model**

Like many temperate gymnosperms, *Pinus x pseudopumilio* exhibits a typical rhythmic growth which can be related to Rauh's model (HALLE & al. 1978: 221–228). Early loss of dominance in the apical meristem of the primary axis (at 2 or 3 years age) results in basitonic branching and is followed by renewed acrotonic branching. This is manifested in the enhanced development of sylleptic branches whose procumbent proximal section and orthotropic section successively develop the typically sabre-curved limb. There are, on the average, 4 to 5 skeleton limbs per individual pine; and these limbs jointly represent the ultimate growth form called “krummholz”. Individual pines are easily studied in the loose stands towards the centre of the bog, and even in closed-canopy stands; individual specimens remain identifiable according to the specific arrangement of their terminal shoots.

The architecture of individual limbs in bog pine is determined by a monopodial axis that grows rhythmically and develops tiers of lateral branches which themselves are morphogenetically identical with the skeleton trunk. Male and female cones are lateral, the former always clustered at the base of the internode (below the set of needle-bearing short shoots), the latter always situated terminally (above the set of needle-bearing short branches).

Rauh's model displayed by *Pinus x pseudopumilio* is very favourable for the architectural

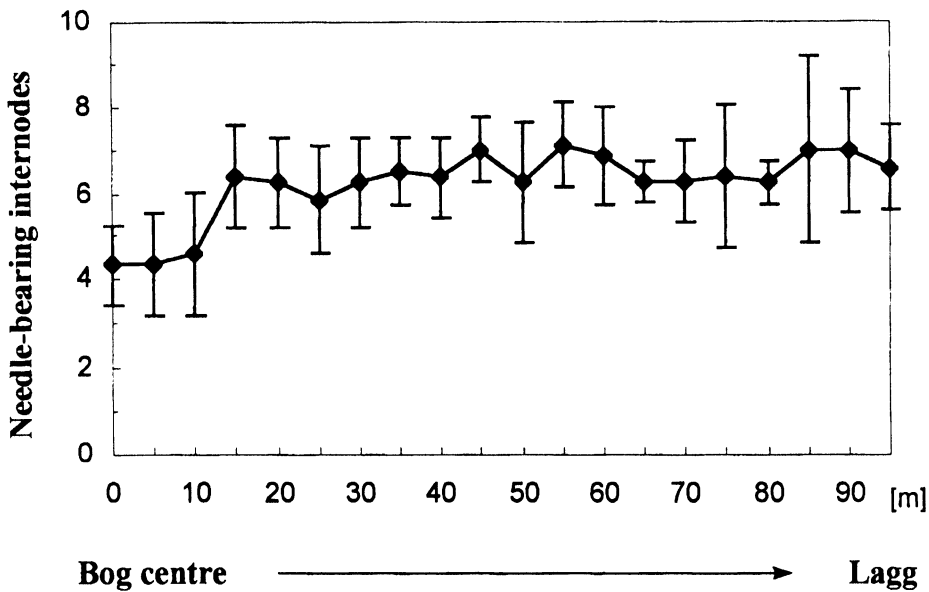


Fig. 2. – Number of needle-bearing internodes (mean with s.d.) on *Pinus x pseudopumilio* along a selected gradient between the bog centre and the lagg of Rokytecká Bog in Bohemian Forest.

analysis, including the identification of age structure, succession of fruiting, persistence of needles, etc. The young stem is clearly fragmented into annual sections marked by (1) extended internodes with short branches bearing the needles (or by scars after the fallen-off short branches), and (2) by distinct „rings“ marked by clustered bud-scale scars. These rings disappear in the thickened periderm only after two or three decades, which enables an easy study of the age structure in individual specimens and whole stands. Presence of several generations of female cones, and obvious gaps left after the male cones also contribute to the easy reconstruction of the reproduction strategy in *Pinus x pseudopumilio*.

In contrast to the studies of ŠTURSA (1966), we were unable to identify stabilised types of growth forms, but further studies in the peatlands of Bohemian Forest may clarify this phenomenon, too. Analysis of the genetical structure of the hybridogenous *Pinus x pseudopumilio* along the environmental gradients will be needed, a task much beyond the range of interests of the present authors.

An important character of the habit of *Pinus x pseudopumilio* is its number of leafy internodes. Earlier observations in Bohemian Forest on Norway spruce (*Picea abies*) proved the effects of air pollution and similar suspicion has been extended with regard to pine species of this area (SKUHRAVÝ 1991). On the basis of our transects, Fig. 2 suggests a range between 3 and 9 leafy internodes per individual limb/bole, with 6 internodes on the average, and significant decrease of leafiness (number of leafy internodes) on the inner margin of the krummholz, towards the centre of the bog.

### Secondary branches

Most individuals of krummholz pine in Bohemian Forest produce secondary proleptic branches (hereafter also „secondary branches“) which arise after one or many later years

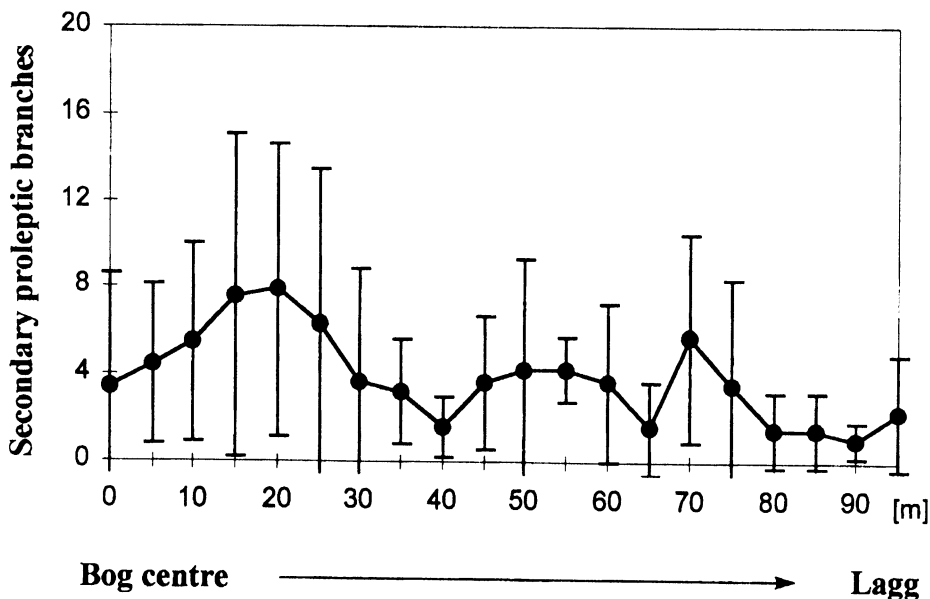


Fig. 3. – Number of secondary branches (mean with s.d.) on individual skeleton branches of *Pinus x pseudopumilio* along a gradient between the bog centre and the lagg of Rokytická Bog in Bohemian Forest.

(1) from the inactive lateral meristems developed simultaneously with the terminal/apical meristem, or (2) from the newly differentiated primordia in the area of the clustered bud-scale scars. In agreement with the characters given by HALLÉ & al. (1978: 42–44, Fig. 2) the proleptic branches can be recognised according to their narrower diameter at the base, short basal internodes and clustered scale leaves. The secondary proleptic branches are mostly short and slender in diameter and bear only a few short-shoots (often only one or two) with a pair of short, often yellow needles. Small, newly arising buds of the future secondary branches can be seen on twigs and limbs of upto 20-years age. Most of the secondary branches thus remain stunted for most of their existence.

Number of secondary proleptic branches occurring on the single skeleton limbs/boles is shown on Fig. 3 indicating a considerable variation of the counts along the whole transect, with averages between 7 and 1 proleptic branch per individual pine. Statistical evaluations did not show any significant difference in the distribution of secondary proleptic branches inside the *Pinus x pseudopumilio* stands. In 1999, the year of our study, similar random occurrence of proleptic branches was randomly observed in stands of Roklanská Bog, and on other mires situated to the east of Roklan/Rachel massif in Bohemian Forest.

Both due to their number and size, secondary proleptic branches do not play a substantial role in the growth form of *Pinus x pseudopumilio*; only occasionally we could observe fairly old and rather thick shoots whose origin was in a secondary branch. In *Pinus mugo*, studied in the sixties by ŠTURSA (1966) in the Giant Mountains, secondary proleptic branches did not play an obvious morphogenetical role.

## Souhrn

Růstová forma stabilizovaného hybridu *Pinus x pseudopumilio* (Willk.) Beck. na vrchovišti Rokytecká slat' na Šumavě se vyvíjí zprvu bazipetálním větvením při ztrátě apikální dominance stonkové osy semenáčku, po němž následuje období akrotonického větvení několika silných větví podle Rauhova architektonického modelu. V souladu se tímto modelem se kosodřevina tvoří rytmickým přidáváním přeslenů „primárních proleptických větví“. Na starších větvích a kmenech, v oblasti „prstěnců“ tvořených nahloučenými jizvami po pupenových šupinách, se ožívují nebo nově vznikají primordia, pupeny a návazně „sekundární proleptické větve“. Tyto větve většinou zůstávají omezené v růstu a mají jen malý počet krátkých jehlic. Počet sekundárních větví nevykazuje ve studovaném porostu statisticky významnou závislost na poloze vůči středu a okraji vrchoviště. Počet olistěných internodií u *Pinus x pseudopumilio* na studovaném vrchovišti kolísal mezi 3 a 9 internodií a byl statisticky významně nižší směrem ke středu vrchoviště.

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