

Succession

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beech undergrowth. A classic example of this kind I have published (4, p. 22) from Subcarpathian Russia, where there exists along the upper forest limit a strip of forest protected by law but where grazing is permitted. These uppermost beech forests possess normally a very rich and typical undergrowth that can be, however, completely destroyed by cattle grazing. So we find, for instance, near the creek Svidovec between Sterešora and the shepherd settlement, Dragobrat, at an altitude of 1200 meters, on the northern side, a pure beech forest where on the ground stamped by cattle, the following species are growing:

<i>Anemone nemorosa</i> (scat.)	* <i>Fragaria vesca</i> (scat.)
* <i>Aposeris foetida</i> (v. ab.!)	<i>Luzula silvatica</i> (only scat.)
* <i>Brunella vulgaris</i> (scat.)	* <i>Myosotis palustris</i> (scat.)
* <i>Caltha laeta</i> (scat.)	<i>Oxalis acetosella</i> (scat.)
<i>Carex silvatica</i> (rather ab., loc. also greg.)	* <i>Parnassia palustris</i> (scat.)
<i>Daphne mezereum</i> (scat.)	* <i>Poa annua</i> (ab. scat.)
<i>Dentaria bulbifera</i> (scat.)	<i>Polystichum Braunii</i> (rarely)
<i>Dryopteris pulchella</i> (loc.)	<i>Rubus idaeus</i> (rarely)
<i>Epilobium montanum</i> (only scat.)	<i>Senecio nemorensis</i> (scat.)
	* <i>Vaccinium myrtyllus</i> (scat.)
	* <i>Veronica officinalis</i> (scat.)

It is obvious that the beech undergrowth underwent a radical change, the most faithful species accompanying the adjoining beech forests are missing, whereas a good many new species (marked with an asterick) made their appearance, among which there is an increasing number of hygrophylous species. This remarkable fact can be explained by the loamy soil, trodden on and trampled by cattle and thus deprived of humus and of a leaf carpet, and consequently becoming considerably more humid.

XVIII. Succession.

As a climax forest community, the beech forests do not undergo, at present, a further succession and I do not know of a single case in which a beech forest gave way, without human influence, to a spruce forest or on the contrary a spruce forest yielded to a beech forest. It is true, that in forests where beech and coniferous trees are mixed, the mutual relation of woody plants during a few gene-

rations may undergo changes which certainly make themselves apparent also in the undergrowth; but here it is more or less only a question of oscillation which does not lead to the ultimate extinction of the beech forest. Transitional types between beech forests and other forests cannot be regarded as stages of succession, because as far as these are not the product of forest culture, they correspond to the habitat. Under *optimal* climatic conditions, the beech forest thrives, without regard to the exposure, all over the mountains from the foot to the tree limit or to the narrow strip of mountain spruce forest forming the forest limit. But there are regions where only special habitats agree with the beech and where beech forests are in close contact with other forest communities. I draw attention to the southwestern foothills of the Carpathians, where beech forests cover the southern slopes to the ridges and oak forests (mostly *Quercetum lanuginosae*) with steppe plant communities (in the first place *Caricetum humilis*, but even small *Stipeta* are not missing), take possession of the southern slopes to the ridges. Here, then, the decision lies in the microclimatic conditions and we are compelled to acknowledge two climaxes, represented by two ecologically and floristically antagonistic forest communities.

Geomorphological formation of the terrain, however, gives rise to habitats of an intermediate character which enables the two forest types, with their accompanying plant communities, to intermingle. These mixed oak — beech forests can be stable, sometimes, however, they lead, in the following succession, to the predominance of one of the communities. But even in this case it is not a question of a succession in a certain direction. The decrease of beech forests from South to Central Bohemia is due to climatic factors.

In mountainous South Bohemia, where the climate is rougher and more humid, beech forests appear on places of various exposure, in the southern part of Central Bohemia they are to be found nearly without exception only in localities with a more or less northern exposure, while towards Praha, on foothills with a warm and dry climate, beech forests disappear, and on the northern slopes they are replaced by mixed deciduous forests with beech and with rather numerous mountain elements in the undergrowth.

On limestone or dolomite in western Slovakia, there originates, in open places of beech forests, rather often *Calamagrosti-*

detum variae and also, especially along ridges and at the foot of rocks, *Seslerietum calcariae*. The first of these communities arise also on clearings created without human influence, but in the next succession the beech regains its footing and the characteristic grassy sociation disappears. In a thin beech forest, replacing a one time *Calamagrostidetum variae*, sometimes the leading grass is still abundantly scattered, disappears, however, completely in the next succession. *Seslerieta*, likewise, can be overgrown by beeches and then they either vanish or they combine with beech elements and form the above described characteristic sociation.

Of less interest is the succession brought about by antropical influences. In our Sudetic-Hercynian region especially, forest culture decimated the original beech forests as well as the mixed forests containing beech and substituted for them mostly cultivated spruce or pine forests. In my book on the Brdy Mts. (1), I gathered data on the change which the forests in Bohemia underwent from historic times to the present. Subfossil findings in Bohemian travertines prove, likewise, the correctness of my deductions, based on historical and geobotanical data.

As a special method for the determination of the original forest types, I have emphasised the study of relic localities and of the remains of beech undergrowth, since this method has proved to be of utmost importance for the reconstruction of the plant covering modified by antropical influences. In cultivated forests, these locally (very often in small clans) preserved species represent the best and often the only indication of the original forest growth. The great significance of even small colonies, as a consequence of the deterioration of the habitat conditions, I have shown by concrete examples. Rather considerable changes occurred in the Hercynian Brdy Mts. in the course of thirty years.

The original undergrowth of beech or mixed forests practically vanished, until at last, in some cases, the Hercynian spruce undergrowth took complete possession of the ground. We have here, therefore, in the forest undergrowth, the following succession due to antropical influence:

Fagetum asperulaceum herbosum (original plant community). Further stages are:

- a) The beech undergrowth is getting poorer, the number of indifferent forest species increases.
- b) Of the beech undergrowth, there remains exceedingly little, newcomers are *Calamagrostis arundinacea*, *Luzula nemorosa* and others, *Vaccinia*, *Deschampsia flexuosa* are still lacking.
- c) In the further succession, there arises a *Luzula nemorosa* or *Calamagrostis arundinacea* type, or *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Festuca ovina* appear, and a spruce undergrowth is finally established. Beech species vanish either completely or are preserved as locally restricted relics. The original rich humus is gradually reduced to acid raw humus, the soil is strongly podzolated, occasionally even an ortstein layer is formed.

Sometimes in cultivated coniferous forests, the beech undergrowth holds its ground for a long period. Thus, I ascertained near Strakonice, on a limestone ridge near Tisovník, in a humous tall-trunk coniferous (mostly spruce) forest, this undergrowth: of beech forest species (and that of deciduous woods), *Cornus sanguinea* (scattered), *Cephalanthera rubra* (v. ab!), *C. alba* (only scattered), *Monotropa hypopitys* (only scattered), *Epilobium montanum* (scattered), *Mercurialis perennis* (abundant!), *Epipactis rubiginosa* (rather scattered), *Hedera helix* (rather scattered), *Aquilegia vulgaris* (only scattered), *Melica nutans* (only scattered), *Athyrium filix femina* (scattered), *Convallaria majalis* (scattered), but also there grow *Luzula nemorosa* (inabundant), *Juniperus communis*, *Scabiosa columbaria*, *Pirola secunda* (abundant), *Polygonatum officinale* (only scattered), *Veronica teucrium* (scattered), and *Calamintha clinopodium*.

On Mt. Svát near Sušice there are, on archaean substratum, pure or practically pure, very humous and shady, rather humid, fir forests, which doubtlessly stand in place of the original beech forest. Beeches are only quite solitary, spruce is interspersed but forms, in places, even growths. In the shrubby undergrowth *Daphne mezereum* grows very rarely, *Sambucus ebulus* very locally, *S. racemosa* on light places. The undergrowth is composed as follows:

<i>Actaea spicata</i> (ab. scat.)	<i>Melica nutans</i> (rather ab.)
<i>Anemone nemorosa</i> (scat.)	<i>Mercurialis perennis</i> (ab.)
<i>Arabis arenosa</i> (ab. scat.)	<i>Moehringia trinervia</i> (scat.)
<i>Asperula odorata</i> (on more places greg., but with diminished prosperity)	<i>Neottia nidus avis</i> (only v. scat.)
<i>Asplenium trichomanes</i> (v. scat.)	<i>Oxalis acetosella</i> (only loc. but greg.)
<i>Dryopteris filix mas</i> (ab.)	<i>Pirola secunda</i> (scat.)
<i>Hedera helix</i> (only loc.)	<i>Pulmonaria obscura</i> (scat.)
<i>Hepatica triloba</i> (scat.)	<i>Veronica chamaedrys</i> (scat.)
<i>Lactuca muralis</i> (scat.)	<i>Vicia pisiformis</i> (v. scat.)
<i>Lathyrus vernus</i> (ab. scat.)	<i>Vicia sepium</i> (scat.)
<i>Luzula pilosa</i> (loc. rather ab.)	<i>Vicia silvatica</i> (very ab.)

We notice that in this case the undergrowth of the coniferous forest is the same as in beech forests. When we find, in the coniferous (spruce) forest (in places abundantly interspersed with hornbeam) at the beginning of the Kamenické údolí valley opposite Klášterec in the district of the Sázava river, a plant community containing *Asperula odorata* (ab.), *Actaea spicata*, *Asarum europaeum*, *Epilobium montanum*, *Hepatica triloba*, *Lactuca muralis*, *Lamium luteum*, *Luzula pilosa*, *L. nemorosa*, *Melica nutans*, *Neottia nidus avis*, *Oxalis acetosella*, *Pulmonaria obscura*, *Viola silvatica*, it is a sure sign that here the original tree was the beech.

It is clear that not all of the above enumerated sociations of our beech forests are climaxes, though the beech forest itself is, in every case, a climax or subclimax.

I have already ⁽²⁾ expressed my opinion on the relations between the Carpathian and Sudetic-Hercynian beech forests. It may, therefore, suffice to say that the latter represent an only floristically impoverished type of the Carpathian beech forests, even if some species (for instance *Galium silvaticum*, *Hepatica triloba*) have their main distribution in the first named region.