ALTITUDINAL VEGETATION BELTS OF THE WESTERN CARPATHIANS

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Conditions determining vegetational zonation

Zonation of montane vegetation was one of the earliest phenomena observed and described in modern ecological science. Plant geographers and ecologists investigated and analysed various aspects of this issue. At present detailed descriptions of vegetation belts are available, including required environmental conditions. It is known that zonation of montane vegetation is basically a result of prevailing climate. The position of the boundaries of altitudinal vegetation belts, particularly of the upper forest limit, is determined by general climate parameters and may be subject to further modifications due to specific factors, such as the general size and shape of rock massifs. However, strong modifications may also occasionally result from topographic features of mountain areas and associated slope processes, particularly at higher inclinations, from the nature of the bedrock or from local soil conditions. Human management, e.g. tree felling, causing the lowering of the upper forest limit, is also likely to be an important factor. The effect of particular factors has been thoroughly studied for the upper forest limit of the Tatra Mountains, on both their Polish and Slovakian sides (Sokołowski 1928). General data on the subject were also provided by Kotula (1989/1990). Specialist studies also addressed local processes associated with zonation (Piękoś 1968, Dzwonko 1976). Altitudinal belts and their variability in other Carpathian ranges (the Beskidy and Pieniny Mountains) were examined in detail as well.

Levels of expression

While characterizing altitudinal vegetation belts the authors most frequently refer to the level of plant communities and consider mainly the ones described as indicator communities. Nevertheless, vegetational zonation is displayed at all levels of floral biodiversity, from the genetic (intraspecific diversity), through the species and community level, to the landscape level. The latter is observed most easily, particularly due to the presence of dominant plant communities and their general appearance, providing a basis for a straightforward distinction between the lower montane beech forest and the upper montane spruce forest, as well as between these belts and the dwarf pine belt or the alpine grasslands. Species of particular herbaceous plants are less visible and more difficult to be noticed in the landscape, especially when small species are considered, not to mention rare ones of infrequent occurrence. Still

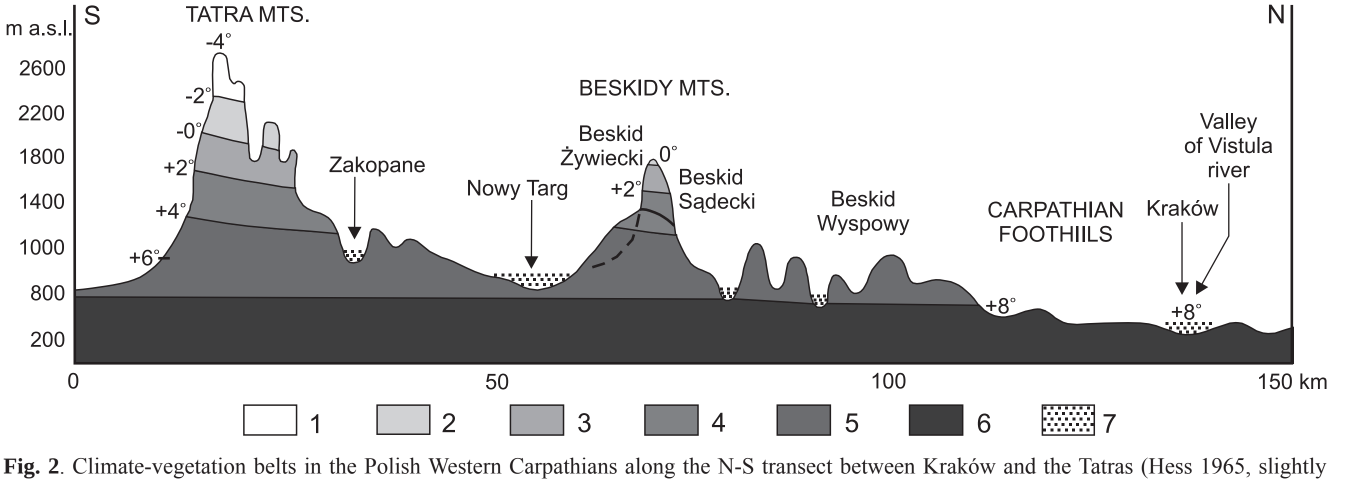


Fig. 2. Climate-vegetation belts in the Polish Western Carpathians along the N-S transect between Kraków and the Tatras (Hess 1965, slightly modified). 1 – cold-subnival belt, 2 – moderately cold-alpine belt, 3 – very cool *Pinus mugo* belt (subalpine), 4 – cool upper montane belt, 5 – moderately cool lower montane belt, 6 – moderately warm submontane belt (= colline belt), 7 – rivers valleys and basins

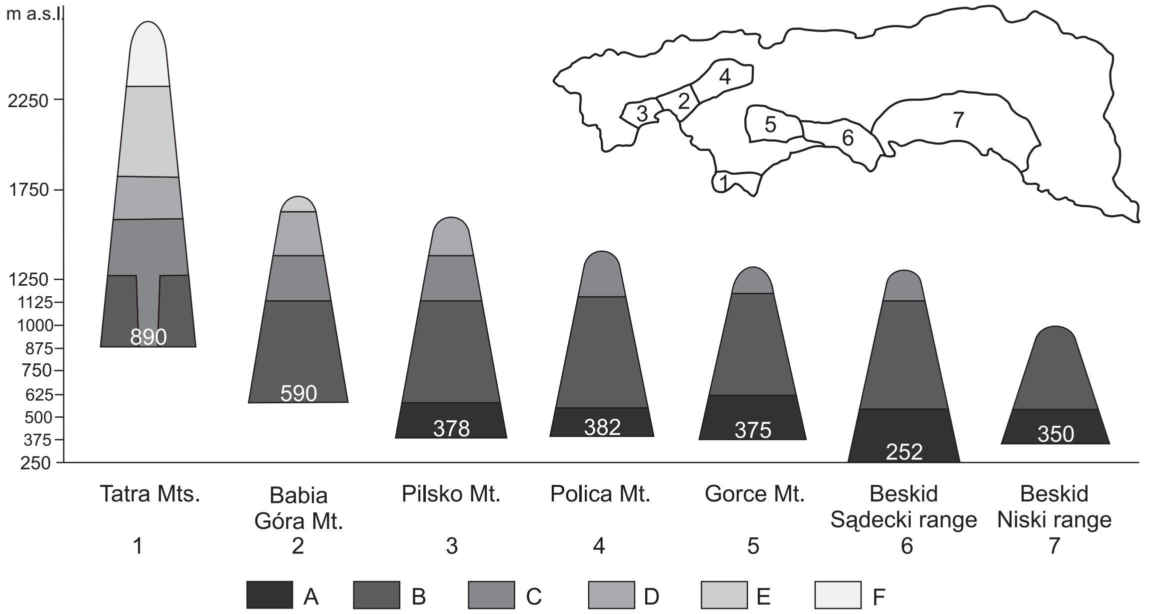


Fig. 3. Altitudinal vegetation belts in single Carpathian ranges (compiled from various sources): A – submontane belt, B – lower montane belt, C – upper montane belt, D – *Pinus mugo* belt (subalpine belt), E – alpine belt, F – subnival belt

less obvious, even to scientists, are the slight differences occasionally observed in terms of the intraspecific variation of particular plants. This phenomenon is mentioned here just for the record, as it is not very important in the description of zonation. However, it is worth mentioning that intraspecific variation is occasionally associated, more or less strictly, with altitudinal climatic-vegetation zonation and contributes to this diversity.

Altitudinal-climatic vegetation belts

As implied by their name there is a critical interaction between variability of climate at different altitudes and associated vegetation belts. For the area of the Western Carpathians studied here, this relationship was described in detail in the source publication of Hess (1965), who presented both a more complete description of climate prevailing in the belt (Fig. 2). Their outline in the main units of the Western Carpathians is given (Fig. 3 and 4).

In the following brief description of vegetational zonation, the species and community levels were emphasized, as these two levels are the main ones considered by palaeobotanists in their attempts at reconstructions of vegetation and its history.

Review of altitudinal climatic-vegetation belts

Figure 2 shows that the main changes in vegetation, which determine the development of distinct belts, are clearly visible in landscape and are recorded altitudinally at an average interval of 300 m, conformable with a ca 2°C change in mean annual temperature.

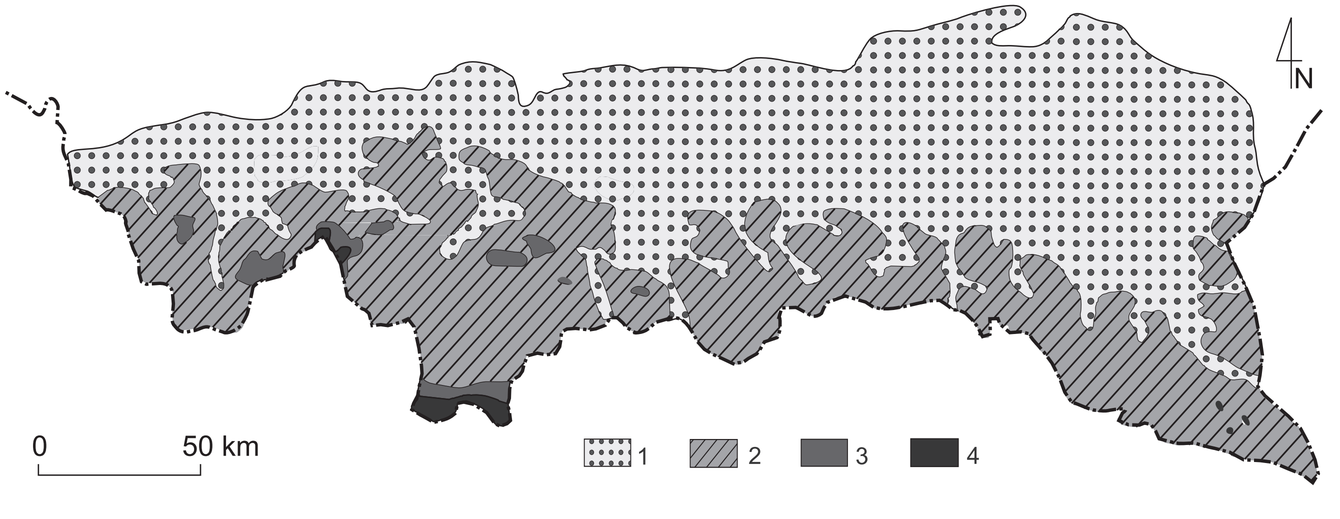
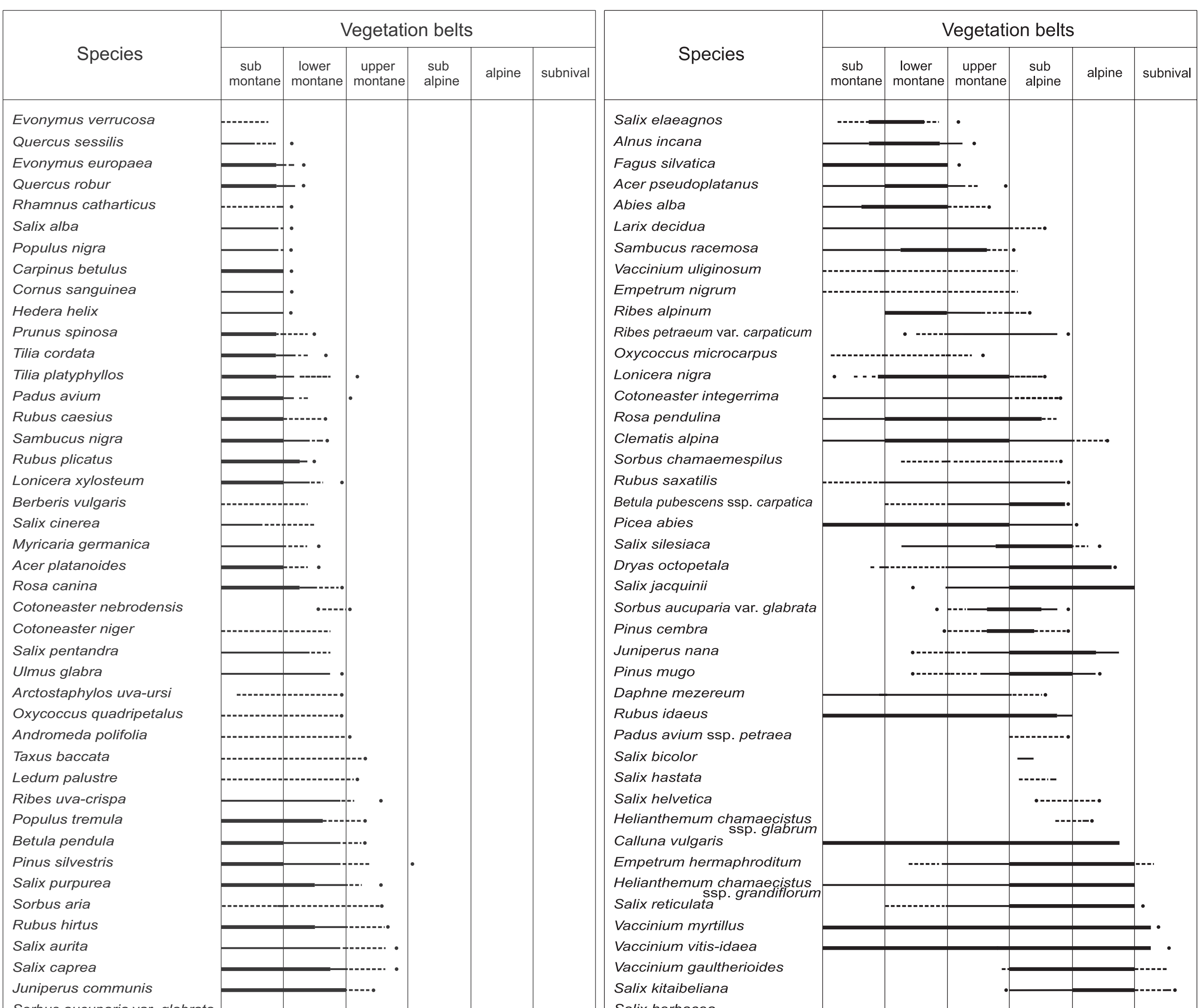


Fig. 4. Horizontal range of the altitudinal belts in the Polish Carpathians; 1 – submontane belt, 2 – lower montane belt, 3 – upper montane belt, 4 – *Pinus mugo* belt (subalpine belt)

The submontane belt

When considering climate, this lowest montane vegetation belt is conformable with a moderately warm climatic belt with a mean annual temperature of 6–8°C (Hess 1965). On average, the submontane belt, extending from the base of the Carpathians (ca 250 m a.s.l.), attains its upper limit between 500 and 600 (mean 550) m a.s.l. However, the differences in the altitudinal range of this belt between the northern and southern slopes, though marked by the same mean value (550 m a.s.l.), may be much higher, even for the same unit. For example, Staszkiewicz (1964) observed in the Jaworz range a 250 m difference in a belt with a 400 m a.s.l. limit on northern slopes and 650 m a.s.l. on southern ones. The indicator forest community of this belt of the Western Carpathians is the colline form of the *Tilio-Carpinetum* association (Pawłowski 1972, Matuszkiewicz W. 2002, Matuszkiewicz J. M. 2008). Areas once covered by such forests are now occupied by secondary grass-rich communities, the so-called oak-hornbeam meadows, representing the *Arrhenatherion* alliance. The belt is also supported by forest associations such as *Luzulo-Quercetum* and the riparian *Carici remotae-Fraxinetum* and *Alnetum incanae.* Other communities are found infrequently and only in very specific conditions, which may be observed for associations such as *Abietetum polonicum* or *Calamagrostio villosae-Pinetum* (growing exclusively in the Nowy Targ Basin) and ones descending from the lower montane belt, e.g. the *Dentario glandulosae-Fagetum*, *Caltho-Alnetum*, *Luzulo luzuloidis-Fagetum*, and *Phyllitido-Aceretum* associations. Forest communities typical of lowlands are found, exceptionally, in very small patches and only at the lowest altitudes. The upper limit of the submontane belt is indicated by numerous species, including trees and shrubs, such as *Carpinus betulus*, *Tilia cordata*, *Quercus robur*, *Acer campestre*, *Salix alba*, *Frangula alnus*, *Euonymus europaea*, *Rubus caesius*, *Rhamnus cathartica*, and

Table 1. Altitudinal ranges of the trees, shrubs and shrublets in the Polish Western Carpathians



herbaceous plants, such as *Typha latifolia*, *Melampyrum nemorosum*, *Dactylis polygama*, *Stellaria holostea*, *Viola odorata*, *Vinca minor*, *Calystegia sepium*, and *Saponaria officinalis* (Tab. 1).

When considering its flora, the submontane belt is dominated by lowland species, but, however, includes minor amounts of montane and colline species. The latter determine the specific character of this belt, being the main area of occurrence of this group of plants. Some of them grow also in the Pogórze Sudeckie Foothills and in upland areas of Poland. Most of the taxa, but much less frequently, also inhabit the lower part of the lower montane belt. Initially, the foothills were a forest belt marked by the dominance of the above-listed communities, in total occupying over 90% of area of the belt. At present, over half of this area is covered by permanent grasslands (meadows and pastures), farmlands and urbanized areas.

The lower montane belt

The lower montane belt develops in areas controlled by a moderately cool climate with mean annual temperatures ranging from 4 to 8°C (Hess 1965). In the Tatra Mountains, where already the base of the mountains is at a level of ca 900 m a.s.l., the belt extends from this level to ca 1200–1250 m a.s.l. In the Beskidy Mountains, the upper limit of the belt is on average located ca 100 m lower than in the Tatra Mountains. However, depending on local and regional conditions, its altitude may vary from 1100(1050) to 1150(1200) m a.s.l. The northern parts of the Tatra Mountains, particularly the carbonate rock formations of the Western Tatras, are inhabited by beech forests, characteristic of this belt. In the High Tatras and their forelands, because of the presence of large areas of moraines rich in crystalline rock debris, numerous sites in this belt are dominated by spruce forests (particularly *Plagiothecio-Piceetum*), characteristic of the upper montane belt. Other important communities include sycamore forests of the *Acerion* alliance and two syntaxa of alder forests: *Alnetum incanae* (along brooks) and *Caltho-Alnetum* (beside local water seepages). Indicator communities of the belt are represented by beech forests, mainly the fertile Carpathian beech forest, *Dentario glandulosae-Fagetum*, as well as, on appropriate soils, by the montane acidophilous beech forest, *Luzulo luzuloides-Fagetum*. The Tatra and Pieniny Mountains are the areas of exclusive and infrequent growth of patches of thermophilous beech forests with orchids (of the *Cephalanthero-Fagenion* suballiance) and fir forests, including both the fertile ones, of the *Galio rotundifoliae-Abietion* suballiance (*Fagion sylvaticae* alliance; *Querco-Fagetea* class), and the lower montane fir forests, *Abieti-Piceetum montanum* (*Vaccinio-Abietenion* suballiance; *Vaccinio-Piceetalia* class). Very small areas are covered by relict pine groves of the *Erico-Pinion* alliance, found in the Tatra and Pieniny Mountains and, very infrequently and in a diminished form, in the Beskidy Mountains. Secondary communities of semi-natural meadows and pastures of the *Polygono-Trisetion* alliance, which have displaced beech and fir forests, and, further, peat bog and tall herb communities, are an important part of landscape in this belt. Minerotrophic mires (the so-called spring-mires), both the obviously more frequent eutrophic ones and the less common oligotrophic ones, are scattered within the entire area of the Carpathians. Typical raised bogs are recorded only in the Tatra Mountains and the Orawa-Nowy Targ Basin, where they occupy large areas as natural communities. Particular regions (the Tatra and Pieniny Mountains) include also high proportions of calcareous alpine grasslands of the *Seslerion tatrae* alliance, developing on strongly exposed, nearly vertical mountain faces. Alpine grasslands occur also on sandstone outcrops in ranges of the Beskidy Mountains, however, far less frequently and in a strongly diminished form (e.g. Granoszewski 1987). In contrast to the submontane belt, dominated by lowland flora and comprising only minor amounts of montane and colline species, the lower montane belt is definitely of a mountain type and includes a greater proportion of montane species within its flora. The frequency of lower montane species, i.e. ones with their centre of occurrence located in this belt and of high-mountain, mainly subalpine, species is of particular importance.

Diversity within the lower montane belt

The lower montane belt extends over an altitudinal range of 600 m and is the most clearly developed climatic-vegetation belt when considering in terms of altitudinal gradient. In fact, it is the only altitudinal vegetation belt which includes two climatic belts, i.e. the lower, moderately warm one, with mean annual temperatures ranging from 6–8°C, and the higher, moderately cool one, with temperatures between 4–6°C. The lower belt is formed at altitudes of 550(600)–850(900) m a.s.l., while the higher one lies between 850 and 1150 m a.s.l. in the Beskidy Mountains or even up to 1250 m a.s.l. in the Tatra Mountains. This division was reported by Pawłowski (1925), who distinguished the two parts, the lower and higher one, within the lower montane belt of the Nowy Sącz region. However, such a distinction was not mentioned in his later publications (Pawłowski 1956, 1972). The diverse nature of the lower montane belt and its division into lower and higher parts was also observed by other researchers (Kornaś 1955, Białecka 1982). The boundary separating the two parts is of great floral importance as its surroundings are characterized by a noticeable disappearance of lowland and colline species. Additionally, above the boundary the proportions of multizonal mountain species do not change significantly, while a notable stable group of high-mountain species appears. If the two parts were not so similar in their general appearance, which results from the dominance of beech and fir with an admixture of spruce, they could be considered distinct belts, of status equal with the other ones. However, in this study they are distinguished as subbelts of the lower montane belt.

The upper montane belt

This belt develops within the cool altitudinal climatic belt, with mean annual temperatures ranging from 2–4°C, and is conformable with the boreal latitudinal climatic-vegetation belt. The upper montane belt is dominated by spruce forests such as *Plagiothecio-Piceetum*, growing in the Beskidy Mountains and in crystalline areas of the High Tatras, and *Polysticho-Piceetum*, found on carbonate rocks of the Tatra Mountains and forming a tiny enclave in the highest parts of the Wysokie Skałki Mountain in the Small Pieniny Mountains. Secondary non-forest communities dominant in this belt include impoverished pastures of the *Polygono-Trisetion* alliance, some types of tall grass meadows and, most frequently, poor grasslands (mat-grass communities of the *Nardetalia* order). Those communities which are natural to a large extent are represented by tall herb communities and, in calcareous areas of the Tatra Mountains, particularly in the Western Tatras, by alpine grasslands of the *Seslerietalia variae* order. Bog-springs, nearly all of the more acidic type, and seepage spring areas are less frequent. At these altitudes, sedge fens virtually include just the *Caricetum rostratae* association, found mainly near postglacial lakes in the Tatra Mountains and in wetlands and boggy sites of the Beskidy Mountains. Communities on deforested areas and locally also bilberry heaths are represented abundantly. The frequency of high-mountain species, particularly of subalpine ones, is notably higher than in the lower montane belt.

The upper boundary of the upper montane belt is determined by an important climatic-vegetation horizon – the upper forest limit. This should be distinguished from the upper tree line, which extends to higher altitudes and links the highest locations where individual spruce trees grow, in this area up to a height of 8 m. The outline and structure of the upper forest limit is strongly affected by various environmental factors, such as climatic (temperature, winds) and topographic features, disturbances (avalanches) and soil types. In the Tatra Mountains, the upper forest limit was thoroughly investigated by several researchers (Sokołowski 1928, Myczkowski 1964, Piękoś 1968, Plesnik 1971). According to their studies, it reaches on average ca 1550 m a.s.l., depending on climatic conditions however its extreme locations may differ greatly. At some sites it descends to altitudes between 1300 and 1400 m a.s.l. and occasionally even below 1300 m a.s.l. The upper forest limit attains its maximum altitudes on the Slovakian side of the High Tatras, on south-western slopes of both the Patria Mountain (1715 m a.s.l.) and the Ostrva Mountain (1670 m a.s.l.). Within the Polish Tatras, the upper forest limit, including spruce and stone pine extends maximally up to 1654 m a.s.l., on the western slopes of the Żabi Szczyt Mountain. Here, according to Matuszkiewicz J. M. (2008), the *Cembro-Piceetum a*ssociation, as distinguished by Myczkowski (1964), actually does not differ from the *Plagiothecio-Piceetum* spruce forest, dominant in the upper montane belt.

The dwarf pine belt

This belt is formed within the very cool altitudinal climatic belt (Hess 1965, 1966) with mean annual temperatures ranging from −2°C to 0°C. In the area of the Western Carpathians, the dwarf pine belt is most abundantly developed in the Tatra Mountains, where, between 1550 and 1850 m a.s.l., it includes dense *Pinus mugo* scrub found on both limestone and crystalline bedrock. Each on the resulting soil types is occupied by a subassociation with a different flora. That found on calcareous soils, the *Pinetum mugo calcicolum* community is more rich and diverse (about 40 species in one average releve), comprising species such as i.a.: *Aconitum firmum*, *Arabis alpina*, *Cardaminopsis halleri*, *Chrysosplenium alternifolium*, *Paris quadrifolia*, *Sedum fabaria*, *Soldanella carpatica* and others. The poorer *Pinetum mugo silicicolum* subassociation (about 20 species in one average releve), typical of crystalline soils, is marked by a less impressive flora, lacking several of the above-listed species. As has been noted for other belts, the lower and upper boundary of the dwarf pine belt, and particularly the upper forest limit, may be found at different altitudes, depending on local climatic and topographic conditions. According to Kotula (1989/1990), the "belt of dense and tall dwarf mountain pine", as he described it, attains its upper limit between 1405 m and 1868 m a.s.l. On northern slopes this boundary is recorded at a maximum of 1750 m a.s.l., while on southern and south-western slopes at 1883 m a.s.l. However, it should be mentioned that the limit of "dense dwarf pine" described by Kotula is located on average 50 m lower than that of the dwarf pine belt distinguished by Pawłowski (1956). Similar differences are observed for the mean altitudes of the lower and upper boundaries of the "very cool" climatic belt, to a large extent conformable with the dwarf pine belt. These boundaries, the lower and upper ones, relate to altitudes of 1550 and 1850 m a.s.l., respectively, on the northern slopes of the Tatra Mts. and visibly higher altitudes of 1650 and 2050 m a.s.l. respectively, on the southern slopes (Hess 1996). The lower limit of the dwarf pine belt is subjected to strong modifications imposed by local climatic conditions and, primarily, by topographic factors, which can be observed particularly in the Tatra Mountains. In gullies resulting from avalanches, the boundary may be lowered by even several hundred meters. The same is true for the

Fig. 5. Disruption and lowering of the vegetation belts in the avalanche gullies – NEE slopes of Czerwony Wierch Mt. above Dolina Jarząbcza valley; seen from the western slopes of Trzydniowiański Wierch peak (Phot. Z. Mirek)

upper limit, because the belt of dwarf pine may not only occur lower but even be disrupted in very steep and frequently disturbed avalanche gullies (Fig. 5). In contrast to this, on rocky ridges, separating the gullies, dwarf pine may be observed at higher altitudes. If its spread was not prevented by competition with forest trees, dwarf pine would most likely also occur at lower locations, as demonstrated by its presence on steep slopes and ledges within the lower montane belt and on the Orawa-Nowy Targ peat bogs, at an altitude of ca 600 m a.s.l.

Pinus mugo, the indicator species of the dwarf pine belt, also grows above its dense belt, just described, in lower parts of the alpine belt, where it extends up to ca 1920 m a.s.l. on northern, north-eastern and eastern slopes and up to 2000–2100 m a.s.l. on southern, south-western and western slopes. Kotula (1989/1990), referring to Wahlenberg (1814), distinguished this area as a distinct “belt of scattered and low dwarf pine”. In this area, the taxon does not form dense masses but isolated patches and is often represented only by individual specimens, with modified growth form and usually not exceeding the height of 0.5 m. Beyond the Tatra Mountains the dwarf pine belt is native only on the Babia Góra Mountain, where it is found between 1350 and 1650 m a.s.l., and on the Pilsko Mountain, where it forms a belt extending from 1300 m a.s.l. to the summit, 1557 m a.s.l. This is also the main altitudinal belt inhabited by high-mountain tall herb communities of the *Adenostylion alliariae* alliance, and, to a large extent, by tall grass communities of the *Calamagrostietalia villosae* alliance. The belt includes also the well-developed high-mountain bilberry and crowberry heaths of the *Loiseleurio-Vaccinion* alliance. Grasslands of the *Nardetalia* order, containing species typical of alpine grasslands and subalpine tall grass communities, are found here as well and form secondary communities commonly occupying areas once used as pasture land, in which dwarf pine was cut or burnt down.

The alpine belt (the belt of alpine meadows)

The alpine belt, described also as the belt of alpine meadows, is formed above the dwarf pine belt and on the Polish side of the Western Carpathians is completely developed only in the Tatra Mountains, at altitudes of 1800 (1850)–(2200) 2250 (2300) m a.s.l. When considering climate, the alpine belt is conformable with the moderately cold climatic belt (Hess 1966), in the Tatra Mountains occupying between 1850 and 2200 m a.s.l. on northern slopes and between 2050 and 2350 m a.s.l. on southern slopes, particularly on the Slovakian side. Beyond the Tatra Mountains, a small patch of alpine belt is recorded on the Babia Góra Mountain, at altitudes ranging from 1650 m up to the summit 1725 m a.s.l. Indicator communities of the belt include alpine grasslands of the *Caricetalia curvulae* and *Seslerietalia variae* orders, occupying areas of crystalline and carbonate bedrock respectively. *Caricetalia curvulae* communities cover larger areas, however both orders are represented abundantly in the Tatra Mountains. On the Babia Góra Mountain, all types of grasslands are found in a strongly diminished form. Among species growing in calcareous grasslands of the alpine belt, the following are worth mentioning: *Sesleria tatrae*, *Ranunculus oreophilus*, *Festuca versicolor*, *Saxifraga paniculata*, *Carex firma*, *Saxifraga caesia*, *Bellidiastrum michelii*, *Dryas octopetala*, *Salix alpina*, *Erigeron hungaricus*, *Pedicularis verticillata*, *P. oederi*, *Minuartia verna*, *Phyteuma orbiculare*, *Androsace chamaejasme*, *Saussurea alpina*, *Oxytropis carpatica*, and *Bartsia alpina*. Grasslands occupying crystalline, poor and acidic soils are noticeably less diverse and are marked by a very similar composition, including the following main species: *Juncus trifidus*, *Oreochloa disticha*, *Festuca airoides*, *Agrostis rupestris*, *Campanula alpina*, *Pulsatilla alba*, *Hieracium alpinum*, *Avenula versicolor*, *Primula minima*, *Huperzia selago*, and, less frequently, *Senecio carniolicus* and *S. carpaticus*. The above-described indicator communities are accompanied by abundant tall grass communities and the less common tall herb communities, as well as by associations inhabiting snow patches, screes and crevasses, all showing a diversity dependent on the nature of the bedrock (limestone or granite). Tall grass communities, covering relatively large areas in the alpine belt, on granite bedrock are represented by the *Calamagrostietalia villosae* order, with the main components being *Calamagrostis villosa* and, at less humid sites, *Festuca picta*. Dicotyledonous species frequently found in tall grass communities include *Gentiana punctata*, *Anemone narcissiflora*, *Solidago alpestris*, *Crepis conyzifolia*, and several others. The most important tall grass community growing on limestone is *Festucetum carpaticae*, formed mainly by large patches of *Festuca carpatica*, occasionally accompanied by species such as *Crepis mollis*, *Dianthus speciosus*, *Linum extraaxillare*, *Phleum hirsutum*, and several others.

The subnival belt

Within the Western Carpathians, the subnival belt occurs exclusively in the Tatra Mountains and only on crystalline bedrock, at altitudes on average exceeding 2250 m a.s.l., extending from 2300 m on southern slopes and from 2200 (exceptionally 2150) m a.s.l. on northern slopes. It develops in the cold climatic belt, which is typified by mean annual temperatures ranging from −4°C to −2°C, and, following Hess (1995), extends from 2200 m a.s.l. on northern slopes and from 2350 m a.s.l. on southern slopes, up to the highest summits: the Rysy Mt., 2449 m a.s.l., in Polish Tatras, and the Gerlach Mt., 2664 m a.s.l. on the Slovakian side. This belt of rocky crags is devoid of large, dense patches of grasslands. They are instead found as small patches at a low density and represent the *Oreochloetum distichae* (*subnivale*) association, including, apart from *Oreochloa disticha*, characteristic species such as *Gentiana frigida*, *Minuartia sedoides*, *Silene acaulis* (ssp. *norica*), *Senecio carniolicus*, *Pulsatilla alpina*, *Festuca supina* (ssp. *vivipara*), *Leucanthemopsis tatrae*, and several others. The belt comprises also patches of tall grass communities of the *Calamagrostietalia villosae* order, snow patches with *Salix herbacea* and communities of the *Androsacetalia alpinae* order, inhabiting mobile or weakly consolidated screes, taluses and granite grits. The order is represented mainly by the *Oxyrio digynae-Saxifragetum carpaticae* association, endemic to the Tatra Mountains and includes species such as, *Cerastium uniflorum*, *Geum reptans*, *Ranunculus glacialis*, *Saxifraga bryoides* and *S. oppositifolia*, *Cardaminopsis neglecta*, *Saxifraga carpatica*, *Oxyria digyna*, and *Cochlearia tatrae*. Within the mosaic assemblage of subnival habitats, the above-mentioned association, on mylonite bedrock (metamorphosed crystalline rocks), is accompanied by the *Seslerieto-Agrostietum* association of the *Seslerietalia variae* order, composed of the following species, recorded also in the alpine belt: *Agrostis alpina*, *Callianthemum coriandrifolium*, *Pulsatilla vernalis*, *Pachypleurum simplex*, *Carex fuliginosa*, *Antennaria carpatica*, *Lloydia serotina*, and several others.