THE PHYSIOLOGY OF PLANTS AT HIGH ALTITUDES[1,2]

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Living conditions for plants in the mountains become increasingly less favorable with increasing altitude. As a result the number of plants which are adapted to these conditions and able to survive decreases. This is a principal reason why the vegetation in the mountains is often clearly segmented into altitudinal levels or zones. While floristic investigation of these levels, their naming, and the first attempt to discover their climatic causes extends back into the eighteenth century, organized research into the relationship of alpine plants to their environment was first initiated at the turn of the last century. The pioneering work in this field was particularly that of Bonnier (1) and of Senn and his students (2) at the alpine laboratory at 2356 m on Muottas Muraigl near Pontresina, Switzerland. In 1926, Schröter (3) summarized the results of these and other early investigations and outlined an extremely fascinating picture of the life and struggles of alpine plants.

With progressive improvement and development of methods for the measurement of the life functions of plants in the field and of the climate in their immediate vicinity (the microclimate), knowledge about the physiology and ecology of alpine plants has become substantially enlarged and deepened. Particularly the investigations of the Botanical Institute of the University at Innsbruck, which have been carried out during the last 30 years under the leadership of Professor A. Pisek, have contributed to this field. We also have Professor Pisek to thank for the last descriptive summary of the life of alpine plants (4, 5) as well as a review on photosynthesis at high altitudes (6).

The following review is limited to those sections of alpine plant physiology which have been most extensively studied.

Climate and Microclimate at High Elevations

We cannot discuss a climate at high elevations as though it were representative of all the world's high mountain chains, since, besides altitude above sea level, the orographic peculiarities, the lay of the land (sun and shade slopes, windy and wind-protected slopes), and above all, the geographical latitude, play decisive roles (7). Nevertheless, we may generalize about certain changes in climate with increasing elevation, at least if we limit ourselves to the mountain ranges of temperate latitudes and ignore those of the tropics (8). Such a limitation is permissible for this review, since the over-

[1] The survey of literature pertaining to this review was completed in August, 1963.

[2] The author wishes to express his appreciation to Dr. Frank Salisbury for his translation of the German manuscript and for valuable discussions relating to alpine plant physiology.

whelming majority of physiological investigations on mountain plants have been carried out in regions having cold winters.

No mountain range in the world has been so thoroughly investigated in respect to its climate from the planes to the pinnacles as have the Eastern Alps by the Austrian meteorologists. The results of this work are compiled in the *Klimatographie von Österreich* (9). The systematic investigation of microclimate at and above the upper forest limit has also made significant progress in Austria during the last decade (10).

Radiation.—Radiation from the sun increases with increasing elevation, since the turbid, scattering, and absorbing atmosphere decreases in mass. For the same reason the diffuse radiation during cloudless weather decreases with elevation. On the other hand, the diffuse radiation increases sharply with elevation when skys are overcast, since the thickness of the cloud layer becomes less. The excess radiation at high elevations compared to the lowlands can be ascribed first of all to this intense, diffuse radiation under cloudy skys (11). In some cases, screening of the horizon and reflection from snow-covered slopes and glacier fields play a significant role in the radiation levels at alpine sites. Thus, on a west slope in the Gurgl Valley (Central Alps of Tirol) at 2000 m above sea level, for example, radiation in summer was only 10 to 20 percent higher than in the lowland, but in the winter it was nearly twice as intense. Seasonal changes in radiation were so unsymmetrical at 2000 m that the level in April almost reached that of July (12).

The highest radiation intensities are not reached under clear skys, but when bright, highly reflecting clouds occur high up. Then intensities at high elevations may climb to 50 percent above those of cloudless skys and well above the solar constant (2.0 cal/cm^2 min). Turner (11) found an absolute maximum of 2.21 cal/cm^2 min at 2000 m. Salisbury & Spomer (13) measured visible intensities of 170,000 lux under these conditions at 4300 m in Colorado (clear sky intensities were 140,000 lux).

Contrasted to this, the long-wave radiation budget is almost independent of elevation (14). Shortwave radiation is decreased more on its way through the atmosphere than is the longer-wave radiation, and thus the blue and ultraviolet portions of the spectrum are significantly lower in the lowland than in the high mountains.

Air temperature.—Air temperature (weather shelter 2 m above ground level) decreases as a rule with increasing elevation approximately 0.5° C per 100 m, and thus at temperate and polar latitudes, the periods during which frost occurs and precipitation falls as snow and stays without melting become longer and the growing season shorter. This temperature decrease with altitude further results in less available heat for the plants during the short summer, thereby inhibiting the rates of many temperature-dependent life functions (e.g., photosynthesis).

Under certain conditions (e.g., an accumulation of cold air in the valleys) a temperature inversion or a hanging layer of warm air with lower tempera-

tures both above and below may develop in mountain regions. According to Baumgartner (15), this is clearly reflected in stem elongation rates of forest seedlings and in the time of appearance of various phenological stages (16). A comparison of temperature minima at 600 or 2000 m showed that at the time of severest winter cold, it was hardly colder at the high elevations than in the lowland (17).

Soil and plant temperatures.—The high incoming radiation in the alpine may, in spite of low air temperatures, result in more heating of soil surfaces and plants than occurs in the lowlands. Thus, Turner (18) reports that the surface of poorly conducting dark soil at 2000 m was heated above 80° C, a value which has yet to be measured in hot, dry desert conditions. It is interesting to note that at the same time, soil surface temperatures of a nearby shaded slope were about 57° C lower; a striking example of how sharply the microclimates of high elevations can vary within very confined areas.

The temporarily high surface temperatures of the soil are also imparted to the lower levels, so that, compared to air temperatures, these become warmer with increasing elevation (14); in an absolute sense, however, the temperatures of the lower soil level decrease with increasing elevation (19).

In winter the soil in the highlands is usually frozen unless it is covered with snow very early so that the cold cannot penetrate. On windy areas where little snow can remain, soil may freeze to a depth of one meter in January and may not thaw until the middle of May (19).

The plants themselves are not heated nearly as much by high incoming radiation, even when the wind is still, as are soil surfaces, since they are cooled more effectively by convective heat transfer. Thus heat damage, even of low growing mountain species, is rare. The crown of the stem at the soil surface becomes warmest, but even this resists the hot surroundings astonishingly well (20).

Tranquillini & Turner (20) recorded needle temperatures of *Pinus cembra* seedlings 10 cm above the soil at 2000 m elevation for an entire year and compared these temperatures with shelter temperatures. Although the average monthly needle and air temperatures hardly differed from each other, the needles at night were noticeably cooler than the air in the shelter, especially in November (at the extreme, 9.3° C). During the day they were heated well above the air, especially in April (at the extreme 21.5° C). In this month the maximum needle temperature was only a few degrees under the maximum for the year. In summer this temperature difference is significantly less. The plants experienced the greatest temperature differences in April (high radiation and low air temperature): the maximum daily amplitude of needle temperature in this month was 34° C; that of the air only 13° C. Temperatures can fluctuate rapidly and widely, as much as 20° C in a few seconds. In April the temperature range, at which the water in the needles of *Pinus cembra* freezes (−4 to −8° C), can be crossed within a few minutes several times in a single day (21). This can lead to damage, even in this exceptionally resistant

woody species (22). Close to the peak of Mount Evans, Colorado, (4300 m elevation) Salisbury & Spomer (13) found the temperature of various leaves to be up to 22° C higher than the air temperature measured in close proximity to the leaves in the month of June.

The high winter radiation in the alpine results in those plants which extend above the snow level having temperatures above freezing surprisingly often. Thus the temperature of needles of *Pinus cembra* exceeded the freezing point at least occasionally on 226 of the 273 days from September to May (83 percent). If we further consider that the ice in the needles begins to thaw at −8° C and is completely thawed at −4° C, then the data indicate that they remained completely free of ice on 42 days during this winter (159 days from October to April), and that they were completely frozen on only 2 days (20, 21). In contrast to this, plant parts which are covered with at least 0.5 m of snow have a nearly constant temperature around 0° C (23).

Wind.—In general, wind velocity increases with increasing altitude, above all when the upper areas of closed forest are left behind. According to Aulitzky (24), the average wind speed in the Gurgl Valley at 3 m above ground just beyond the upper forest limit (2000 m) is 40 percent above that at the valley floor (1800 m). At the tree line 200 m further up, velocities were 70 percent of those in the valley.

One can see the effects of strong wind especially distinctly on knolls and ridges which are exposed to it: the trees exhibit typical wind forms and dwarfing; the shrubby vegetation is also mechanically damaged; the soil is eroded; and in winter the soil is free of snow. Only a few wind and drought resistant species can colonize such sites.

On a much larger area of the mountain surface, the wind is diminished by the screening effects of relief, especially close to the plant cover. Thus, Stocker (25) found wind velocities from 0.5 to 4.0 cm/sec between *Calluna vulgaris* plants (alpine heather) compared to 340 to 460 cm/sec one to two meters above the plants. Warren Wilson (26) obtained similar results. In winter the wind is more noticeable close to the snow surface, since friction against this smooth surface is considerably less (27).

In general, the effect of wind, especially summer wind, on plants is overestimated. Plant temperatures as well as transpiration and photosynthesis are directly influenced by the wind only up to relatively low velocities (28, 29, 30) and remain constant as the velocity further increases. With long exposures to wind, however, the water status of the leaves is impaired, leading to a narrowing of the stomatal openings and a reduction in transpiration, CO_2 uptake, and dry matter production (26, 29).

Humidity and evaporation.—With increasing elevation the vapor pressure (absolute humidity) of the air decreases, so that, on the average, at 2000 m the air contains only half as much water vapor as at sea level. According to Rathschüler (31), this gradient is especially pronounced at night, the differences becoming smaller during the day. With increasing altitude air tempera-

ture drops, and with falling temperature the saturation pressure of water vapor decreases sharply. Thus, although absolute humidity decreases, relative humidity increases and the saturation deficit decreases with elevation.

Since evaporation is also dependent upon radiation and wind velocity (32), and both increase with elevation, only comparative measurements with standard evaporimeters can determine whether or not plants in the mountains are exposed to a greater evaporating power of the atmosphere than in the lowlands. Walter (33) has assembled the meagre references to work at high elevations. From these it is apparent that evaporation at high altitudes is hardly higher than at lower elevations. Maxima of 1 cm^3/hr (Piche-evaporation, green disks, 3 cm diameter) are as a rule not exceeded, according to measurements of Prutzer (34), even on wind-exposed ridges at 2000 m.

Precipitation.—Precipitation increases with elevation up to the nival level (upper limits of closed alpine meadow), especially in the precipitation-rich border zones of a mountain range (35). From average data of 230 weather stations in the Northeast Alps, the yearly precipitation sum doubles as elevation increases from 700 to 2300 m (36). The amount of precipitation received by a mountain station is, however, strongly dependent upon how it is exposed to the winds which bring rain, or protected by topography from these winds.

In the Eastern Alps, maximum precipitation falls in summer (in the Gurgl Valley 60 percent of the yearly total falls in the summer half of the year). This precipitation is distributed over the summer with remarkable uniformity. It rains on the average every second day during summer. Periods free of precipitation never last long, on the average 4 days, in the extreme 14 days. The result of this is that the soil in the mountains remains continually moist. Unfortunately, continuous records of soil moisture in the Alps are lacking, but according to Neuwinger-Raschendorfer (37), the soil on the windward north side of a ridge dries out more rapidly than on the sunward lee side. In the distinctly more continental climate of the Colorado Rocky Mountains, extended dry periods do occur during the growing season (38). Spomer (39) describes a period from the middle of August to the middle of September 1960 during which the soil moisture content measured at 15 and 30 cm depths at several alpine stations remained below the wilting point.

Snow.—Due to decreasing temperature with increasing altitude, there is a general increase in the number of days on which snow falls, and concurrently the yearly sum of new snow depth, the number of days with snow cover, and the maximum snow depth. In particular, the snow depth and the duration of the snow cover in the mountains are dependent upon orographic position (35) and micro-relief (40). The snow is continually blown off of parts of the terrain exposed to the wind and accumulated in nearby depressions. And the deeper the snow drift, the longer it will last into summer. These differences in snow cover have a sharp selective action upon the vegetation. Extremely short snow cover can only be tolerated by plants which are resistant not only to cold but also to long periods of drought; extremely long snow cover only by

those which can complete their development in a short snow-free period and are not susceptible to parasitic snow fungi (41).

Transpiration

The transpiration of numerous plants of the alpine zone has been thoroughly investigated, particularly in the vicinity of Innsbruck (42–46). Among the tested species, there are those with high as well as those with low specific transpiration, and this is true even among the cushion plants, a group having very uniform physiognomy (47). In addition, there are plants which on clear days reduce their transpiration at noon, while others transpire linearly with evaporation, producing a transpiration curve with only one peak.

The plants of the alpine zone cannot be fundamentally separated from those of the lowland in either capacity or behavior of transpiration. If, however, transpiration of plants from various alpine habitats is compared, then characteristic differences become apparent: plants on scree slopes (rocky rubble) exhibit the highest transpiration (*Rumex scutatus* reaches 12.3 g/g fresh weight on clear days, a water turnover accomplished by only 3 of the 68 other alpine and lowland species which have been investigated). These plants also show a distinct restriction of transpiration towards noon, which suffices to keep the plants in balance: the water content of the leaves hardly changes throughout the day, and osmotic values remain low. This compensated balance in spite of high transpiration allows us to conclude that the plants as a rule encounter rich water sources in the fine earth under the rubble. The layer of air in the rocks protects the fine soil lying below from drying out, and in addition, the root system of these scree plants is extensive, since they have a large volume for growth at their disposal [see below and (48)].

Plants on snow bank areas transpire significantly less, but in contrast to the group just discussed they do not restrict transpiration at midday. The soil is continually kept moist by melt water coming from the snow bank above (49). The unrestricted transpiration results in higher osmotic values (average 13 atm) than in the scree plants (average 10 atm) (50). Apparently, as an adaptation to the very short growing season which is available for dry matter production, stomates remain open during the day, allowing continuous CO_2 uptake, but an impaired water balance is purchased in the bargain.

The evergreen dwarf shrubs exhibit a particularly low transpiration but are thus able to transpire almost parallel with evaporation. Their noticeably higher osmotic values (average 17 atm) could be genetically determined.

Water Consumption

Besides specific transpiration, the transpiring leaf mass per unit soil surface area determines the water consumption of a plant community. According to Pisek & Cartellieri (45) and Vareschi (51) the production of plant mass as well as the collective plant surface area of communities in the alpine is

generally low, particularly in the open vegetation of rock debris (50 to 60 g fresh weight/m^2). Significantly larger masses can be found on snow bank soils (280 g/m^2), although the typical colonizers of these habitats are highly dwarfed. The largest masses to be found among the alpine associations are produced by the closed dwarf heather (500 to 1000 g/m^2). Compared to this, the mass production of a xeric meadow on the plains may be 500 g/m^2, that of a mesic meadow 1500 g/cm^2. If, from these data, the amount of water given off is calculated on a square meter basis for a clear day, it becomes apparent that the various rates of water turnover by the specific vegetation units is determined more by the mass production than by the specific transpiration of the plants making up the stands. Thus a unit surface area of scree vegetation transpires less water, in spite of a high specific transpiration of its individual plants, than the dwarf heather, with the exceptionally low transpiration of its individual plants. Similar results were obtained in a comparison of total CO_2 uptake of *Larix decidua* and *Pinus cembra* trees at timberline (52) as well as by a comparison of water turnover rates in dry regions (53).

Pisek & Cartellieri (45) also calculated the yearly water turnover of various plant communities and compared this with the yearly precipitation. Even the dwarf heather, which is at the top of the alpine communities, transpired only 200 mm per year, which is one third of the summer and one fourth of the yearly precipitation in this region.

Water Balance

Summer.—The water loss of alpine plant communities, which is low compared to yearly precipitation, and the evenly distributed summer precipitation usually result in the alpine plants having a well distributed water balance during this season, and they are never in danger of drought (50). Osmotic values of alpine plants lie somewhat lower than values for comparable plants in the lowlands. Only during a three-week dry period in August—a great rarity at high elevations—is there an increase in osmotic values due to water loss, especially in sunny dwarf heather stands (50).

Winter.—Plants or plant parts which are covered with snow in the winter lose no water, since the atmosphere in the pores of the snow is water saturated. Even when the soil is frozen, leaves can make up the water deficit which occurred before they were snowed in by absorbing vapor from the air (54). At the time of melting, plants can slowly take up water from the soil, so that their water content is nearly saturated shortly before they are set free from the snow, and their osmotic values have dropped to the summer low (23).

The winter water balance of large evergreen trees at timberline is also well equalized. All studies agree that their stomata are closed during the entire winter (23, 46, 55), and their transpiration is therefore extremely low. They are deep rooted and thus reach soil levels which remain mostly unfrozen. In addition, they have large water reserves in the branches and in the

trunk. From the standpoint of water balance, it would be important to know if they can use this water, or if the water columns in the branches and trunk are broken in the winter. According to Michaelis (56), the water in thin branches might thaw whenever the needles are heated above 0° C by strong radiation, since the branches also are quickly heated. It is more difficult to answer the question of whether or not water transport from the trunk is also possible under these conditions. The water in the vessels can be supercooled to −9° C, but in nature it is always frozen at these temperatures (57). The freezing point lies, depending upon the object and the test method, just a few degrees below zero (56, 58, 59). According to Michaelis (56), parts of the trunk in direct sunlight become heated relatively rapidly in late winter to above the freezing point, but shaded parts thaw only after a series of frost-free *föhn* (Chinook) days. According to Lybeck (57), gas bubbles may form in the vessels upon thawing, and these might hinder water conduction.

The environmental problems are much more severe for the smaller trees above the upper forest limit (transition zone) and for evergreen shrubs in late winter, especially on locations where the snow melts early or where it is frequently blown away in winter. In such cases the water loss is considerable in spite of closed stomates, since the plants thaw out almost daily and since they are heated well above the ambient temperature by intense radiation. Yet the air is still cold and thus dry (large vapor pressure gradient). Obtaining water from the soil is usually impossible, since it is frozen. Thus the water balance continues to become worse with advancing winter, as can be seen by a sharp climb in osmotic values (50). Frequently the damage point is reached (frost drought).

This damage increases rapidly with altitude above the upper forest limit, on the one hand because the climate becomes increasingly extreme, and on the other hand because seasonal growth does not progress to maturity due to the short growing season (less cuticular protection against transpiration) (23, 60, 61, 62). Schmidt (63) even sees this as the principle cause of tree line in the Central German mountains. According to Gäumann & Peter-Contesse (64) the wood of *Abies alba* tends to be increasingly less perfect as the altitude increases and thus more easily attacked by fungi and more subject to rot.

The dwarf shrubs vary considerably among themselves in their ability to survive the winter dry period: *Rhododendron ferrugineum* twigs that are denuded of snow in late winter wither within a few days. Their cuticular transpiration is relatively high and their drought resistance low. *R. ferrugineum* is therefore dependent upon snow protection and is (with *Vaccinium myrtillus*) a certain indicator of late lying snow. *Calluna vulgaris* and *Empetrum nigrum* respond in much the same way.

Surprisingly, *Loiseleuria procumbens* tolerates the winter drought well on areas which are extremely exposed to the wind and which therefore remain free of snow during the winter. The water content always remains safely above the value at which the leaves are lethally damaged. According to

Larcher (65), they are able by the use of adventitious roots to take up the melt water of late winter which cannot penetrate the frozen soil but saturates the ground litter and humus.

Frost Resistance

The damage which is frequently observed, especially in late winter, can be caused by either winter drought or freezing. It is not easy to determine which of these two causes might be decisive. Ulmer (66) investigated the frost resistance of numerous plants growing at the upper forest limit in the Alps. Frost hardiness of the leaves varies in the course of the year, being minimal in summer. This is especially true of newly formed leaves, even if they are fully grown. Resistance climbs rapidly and reaches a maximum in early winter. Sugar content and the osmotic values of the cell sap run closely parallel to this, yet these changes are not necessarily causes of the different sensitivities of the leaves to cold (67).

The yearly curve of frost resistance is of course determined by the temperature history of the plant before testing. In addition, it has been suggested that this curve may be influenced by an internal annual rhythm. This seemed especially likely since dehardening could be detected during the spring in branches taken from under the snow, where temperature remains essentially constant (66, 68). Such a rhythm may well exist, but as yet the possible effect of changing day length has not been eliminated as a controlling factor, and it is indeed known that changing photoperiod in a greenhouse influences frost resistance (short day increases resistance) (69), and drought resistance is known to respond in the same way (70). In the field, frost resistance increases in late summer, although the temperature remains high. In addition, the readiness of plants to change their frost resistance in response to warm or cold treatment differs with the various seasons. Hardening is most successful in fall while dehardening works best in late winter (71). These effects could be either a response to changing day length or to an internal annual rhythm.

Of the plants of the upper forest limit investigated, *Pinus cembra* was superior to all others so far as frost resistance is concerned. In midwinter it can endure at least −42 C when this temperature is given for 2 hours, with cooling and warming times of 2 to 5 hours. With shorter times at the minimum and very slow cooling and warming, other *Pinus* species can even survive significantly lower temperatures (72). Other species are able to tolerate nearly as much cold: *Picea excelsa* and *Pinus mugho* (−38° C), as well as *Loiseleuria procumbens* and *Juniperus nana* (−36°C). *Calluna vulgaris*, *Arctostaphylos uva ursi*, *Carex firma* and *Saxifraga caesia* are damaged at temperatures between −30 and −26° C, while *Vaccinium vitis idea*, which is frost resistant to −24° C, forms a transition to the frost sensitive plants that freeze at temperatures higher than −20° C and are thus limited to snow protection at the forest border (*Erica carnea*, *Globularia cordifolia*, *Homogyne alpina*). *Rhododendron* is also included among these (71). Readiness to

be frost hardened or dehardened also varies from species to species. *Picea* and *Loiseleuria* are very stable, *Pinus cembra* somewhat less so, while *Rhododendron* can be hardened or dehardened easily and extensively.

These studies demonstrate that, with the exception of the plants depending upon snow protection, the plants are well adapted to the winter temperatures of the high mountains. It must also be remembered that in the night, the leaves, especially those close to the snow surface, become significantly cooler than the air. Late frosts can be dangerous for all alpine plants, since the leaves are strongly heated in late winter, resulting in the initiation of dehardening. Yet the causes of the frequent late winter damages to alpine plants can only be determined with difficulty, since at this time the danger is highest for damage either by drought or by rapid freezing and thawing.

PHOTOSYNTHESIS

We shall next consider the extent to which photosynthesis of alpine plants might be adapted to high elevations (high light intensity, low temperature, and low carbon dioxide partial pressure).

Dependence upon light.—We have known since Lundegårdh (73) and Boysen Jensen (74) that sun species require more light for both photosynthetic compensation and saturation. The suspicion that in alpine plants these two cardinal points of the light dependency curve for photosynthesis are pushed still further in the direction of high light intensity so that these plants can make even better use of the available light quantities has been confirmed by Cartellieri (44). This is especially true of *Ranunculus glacialis*, which is found at higher altitudes than any of the flowering plants in the Alps (75): its net daily carbon dioxide profit climbs proportionally to the daily light total and is highest on days with clear skies.

According to Mooney & Billings (76), photosynthesis of *Oxyria digyna* continues to increase at 56,000 lux when plants are collected at 3740 m, while photosynthesis of plants collected at 1740 m is already saturated at 22,000 lux.

Using high mountain plants from the Pamir range in Russia, Glagoleva (77, 78) found light saturation only at intensities of 75,000 to 90,000 lux, which is 50 to 60 percent of maximum field intensities. She ascribed these high values to the thickness of the palisade tissue (5 to 6 layers). With other plants photosynthesis continued to increase up to the maximum illumination level (150,000 lux). Since her measurements were, however, made using the unnaturally high carbon dioxide content of 0.3 to 1.0 percent, they cannot be compared with the values mentioned above (44, 76). It is well known that the values for light saturation increase as the carbon dioxide content increases (79).

Temperature dependence.—Pisek & Winkler (80) found the temperature response curve for net photosynthesis of various plants always to have a

single peak. The position of the cardinal points (minimum, optimum, and maximum) varies from species to species, and even within one species they may be shifted. Thus, the higher the light intensity the higher the optimum and maximum for the same plant.

Tropical and subtropical plants seem to be adapted to a warm climate in that their temperate optima lie distinctly higher (25–30° C) than those of plants in temperate latitudes (15–20° C) (81). Conifers in the valley assimilate maximally, depending upon light intensities, between 15 and 18° C. At tree line the temperature optimum lies 2 or 3 degrees lower (80).

The temperature minimum for net photosynthesis of various northern alpine evergreen plants lies between −2 and −5° C, according to Pisek & Rehner (82). In this temperature range the water in the leaves of *Pinus cembra* begins to freeze (21). Probably, photosynthesis must stop because water is drawn out of the cells by freezing. Holzer (83) observed a distinct flattening of the chloroplasts in winter. Other factors could be taking part, however, such as stomatal closing due to cold and irreversible decreases in the activity of enzyme systems essential for photosynthesis (84). In contrast to these results, Godnev & Rotfarb (85) were able to demonstrate the presence of C^{14} in the sugars of the needles of *Picea excelsa* after they had been exposed for several hours to −14° C and then treated at the same temperature with $C^{14}O_2$.

Recently, Lange (86) found an unusually low temperature optimum and minimum for photosynthesis of alpine lichens. The temperature optimum of *Parmelia encausta* lay, for example, between −10 and 0° C, the minimum for *Stereocaulon alpinum* at −23°C. With these species photosynthesis is not inactivated even when they are exposed for 15 hours to −30° C. After just a few hours at temperatures above 0° C the capacity to initiate photosynthesis can be restored. Apparently, the algae in the lichen thallus are much less sensitive to water removal than the assimilating cells of vascular plants. This attribute may be the reason why lichens are able to colonize at elevations above those where flowering plants grow. They are the uppermost pioneers of vegetation. *Umbillicaria* species have been found in the Himalayas up to 6200 m.

Dependence upon carbon dioxide partial pressure.—As elevation increases, the carbon dioxide partial pressure decreases (6). This provided a motif for the suspicion that carbon dioxide partial pressures might play a deciding role in the altitudinal zonation of plants in the mountains. Various other factors are certainly involved, but Billings, Clebsch & Mooney (87) have indeed shown that, under standard conditions, *Oxyria digyna* plants collected at 2027 m can assimilate more under low carbon dioxide partial pressures than comparable plants collected at sea level. At 0.4 mg CO_2/l (comparable to the carbon dioxide partial pressure found at 3000 m), the plants collected at sea level were capable of only 70 percent as much photosynthesis as those collected in the mountains.

Respiration

According to Pisek & Winkler (17), *Picea excelsa* branches at tree line respire more over the entire temperature range in both summer and winter than do branches in the lowlands—in summer about 50 percent more. This high specific respiration of mountain trees, however, can hardly produce an unfavorable carbon balance, since the temperatures at the elevations where they grow are nearly always low. For this reason the night respiration of trees at timber line during the growing season are substantially less (52, 88) than their counterparts on the planes (89).

Annual Photosynthetic and Respiration Capacity

Net photosynthesis of conifers varies from late fall into spring when it is tested in the laboratory under standard conditions of light intensity and temperature ("photosynthetic capacity") (17, 90, 91). In addition to the water status of the plants, a number of factors might be involved in this change in photosynthetic capacity, such as after effects of the previous temperature conditions to which the test plants had been exposed as well as an endogenous annual rhythm. The first frosts in the fall which freeze the water in the needles have a lasting inhibitory effect on the photosynthetic capacity. As frosts become sharper and more frequent, photosynthesis is finally stopped. Tranquillini (23) was able to show that in late fall the net carbon dioxide uptake of *Pinus cembra* seedlings at tree line on successive test days having approximately equal total radiation values was less the more severe the frost had been during the previous night. Zalenskij (92) and Philippova (93) also found that the rate of photosynthesis climbed only slowly on a day following a cold night.

Respiration is also reduced in midwinter, when it is measured at the same temperature as plants in summer. This is considered to be proof that the plants are in a condition of true dormancy. Respiration capacity, however, climbs much more rapidly during a short warm period than does photosynthetic capacity, and thus the test branches continue to evolve carbon dioxide in midwinter, especially on warm, *föhn* days.

As an indication that winter dormancy is induced not only by temperature conditions but also by other factors are the facts that photosynthesis can never be increased in midwinter to the summer level by treatment with high temperatures (17) and that plants kept in the greenhouse under frost free conditions also show a drop in photosynthetic capacity (69). Changing day length should be investigated as a contributing factor here, since it is known to initiate true dormancy in trees at lower elevations (94).

As the weather warms up in the spring, and night frosts become less frequent, the photosynthetic capacity slowly climbs. If trees from various elevations are compared over an entire year, it becomes clear how deep and long photosynthesis is repressed by the longer frost period at high altitudes (17).

This is undoubtedly one of the main reasons why an upper altitudinal boundary exists for the forest, for tree growth in general, and for the existence of higher plants (92).

The time of transition from winter dormancy to summer activity appears to be under genetic control. *Acer rubrum* plants grown in a garden broke dormancy earlier if their seeds came from regions with a short frost period (95) compared to those from regions with a long frost period. For the same reasons, the higher the altitude from which seeds come, the less the growth of the seedlings under otherwise comparable conditions (96, 97).

Dry Matter Production and Assimilation Economy

One might expect that the short growing season must be intensively utilized by alpine plants, whether it is due to long snow cover, late sprouting and early leaf fall (summer green plants), or the length of the winter dormancy period (evergreens). The results of all investigations in the high mountains agree with this, showing that plants there assimilate strongly (98). According to Glagoleva (77), the maximum potential net photosynthesis of various plants in the Pamir at 3860 m under carbon dioxide saturation was up to twice as high as at 2350 m, although there was no further increase at 4780 m. The peak values, which are not strictly comparable (79) to results of other authors who used normal carbon dioxide partial pressures (44, 76), lie at 200 mg/g dry weight/hr (*Primula algida*), although there are other species which assimilate significantly less (*Stilphonophleum anthoxanthoides*, about 30 mg/g/hr).

Cartellieri (44) found for three herbaceous species from silicate scree slopes at 2600 m in the Alps (*Sieversia reptans*, *Doronicum Clusii*, and *Ranunculus glacialis*) hourly yields between 18 and 27 mg per dm^2 of simple leaf surface. In contrast, sun plants at low elevations reach only 10 to 20 mg/dm^2, and shade plants only 4 to 16 mg/dm^2. Only cultivated plants give values as high as 20 to 30 mg/dm^2 (81). The average daily total of the three plants studied by Cartellieri was about 150 mg/g of leaf dry weight. This corresponds to a carbon gain of 40 mg. Since the carbon content contributes to about 50 percent of the dry weight, 80 mg of carbon are added daily to each gram of carbon already present. This means that a leaf produces in about 15 days the substance for an identical leaf (losses through night respiration are already taken into account). Since the dry weight of the petioles, flowers, and fruits, as well as the stem tissues, is at most no greater than that of the leaves, such plants require hardly more than a single bright month free from frost and snow to accumulate material for the next year's growth.

The growing season for these plants lasts about three months. Thus, Cartellieri's investigation shows how plants having such a short growing season are nevertheless, because of a high specific photosynthesis and ability

to utilize the light, quite able to complete their growth. There is no shortage of assimilates.

The assimilate economy of three perennial herbs in Wyoming at 3300 was studied by Mooney & Billings (99). The growing season there is still shorter, lasting just a little over two months. When the plants go into dormancy their underground organs (roots, rhizomes) are filled with reserve materials. When growth is again initiated, partially under the snow and partially immediately after the snow melts, these reserve materials are largely used up in the formation of the shoots. Shortly thereafter, however, as a result of intensive photosynthesis, carbohydrates again begin to be stored, and the content continues to increase. Even at the time of greatest use there are still reserves available which might keep the plants from starving in years having an extremely late snow melt. On areas which became free of snow later than the middle of July, plant cover was extremely reduced and primary production was essentially nil (49).

Chlorophyll Destruction

Montfort (100) discovered that in the leaves of many plants synthesis of chlorophyll is inhibited by sunlight, and existing chlorophyll is extensively destroyed, so that the chloroplasts in the upper layers of the palisade layers regularly fade out. This photosensitivity appears to be genetically determined (plants which are stable in the lowlands, e.g., *Silene inflata*, remain stable in the mountains), and such sensitivity is not limited just to plants that occur in the lowland. Thus, alpine species such as *Globularia cordifolia* and *Adenostyles albifrans* are distinctly photosensitive.

Evergreen conifers in winter become especially sensitive to high radiation and suffer considerable loss of chlorophyll, particularly at high elevations. Some protection against this is provided by migration of the chloroplasts either to the middle of the cells, where they become concentrated around the nucleus (*Picea excelsa*) or into the corners of the fold parenchyma (*Pinus cembra*) (83, 101). Nevertheless, in winter so much chlorophyll is destroyed in needles on the sunny side of the tree crown or on the sunny side of individual needles, that they become distinctly yellow to the unaided eye. It has been shown, however, contrary to earlier opinion, that even under extreme conditions in winter the chloroplasts always remain entire and are not dissolved (83, 101, 102).

The loss of chlorophyll, which according to Tranquillini (23) may lower the chlorophyll content of needles exposed to the sun (*Pinus cembra*) to one third of the summer maximum value, sharply reduces the photosynthetic capacity of the needles which are involved. In late winter, yellow colored branches commonly have a negative carbon dioxide balance. They first regain the ability for normal photosynthesis in spring after the chlorophyll content has increased in response to warm weather (23).

Resistance to Ultraviolet Radiation

Pirschle (103) studied the growth of plants from various elevations in growth chambers at constant temperature, moisture, and light, with and without the addition of artificially produced long-wave or middle-wave ultraviolet light. It was apparent that the plants which received long-wave ultraviolet light were indeed somewhat inhibited in their elongation compared to those receiving only visible light, but no damage was suffered by any of the plants. Irradiation with middle-wave ultraviolet (UV-B, Dorno region, high elevation UV, 280 to 315 mμ) resulted in death after a short time of plants from sea level (*Stellaria media*, *Silene maritima*), whereas alpine plants remained alive. Elongation and dry matter production were less reduced the higher the elevation from which they originated.

Brodführer (104) attributed the damage in the experiment of Pirschle to shortwave ultraviolet wave lengths contained in the light source. She exposed various plants to the natural radiation at 1600 m and found an inhibition in growth but no damage to the plants.

According to Lautenschlager-Fleury (105) the ultraviolet resistance of plants in the high alpine rests upon a filtering action of the upper epidermis. Ultraviolet transmission was less the more intense the light in which plants were grown. Only visible light and not ultraviolet radiation itself influences the subsequent transparency to ultraviolet. For this reason the leaves are damaged the most when they are irradiated with ultraviolet alone. The marked filtering action of the epidermis against ultraviolet is ascribed to the cell sap and not to the cell wall. Shortage of carbon dioxide and darkness increase the ultraviolet transparency. Thus, absorption of ultraviolet may take place through products of photosynthesis.

Growth and Development

Growth and flowering of alpine plants is presently being studied in the field and growth chambers. For example, Billings and his students (76), who might be considered the pioneers in this area, have shown that *Oxyria digyna* responds to photoperiod according to its geographical origin. All samples in a latitudinal series extending from California and Colorado to Greenland and Alaska flowered in response to long day, but the farther north the plants were collected, the longer the day length required to initiate flowers. Formation of perennating buds was also found to be under photoperiodic control. Salisbury and his students have also initiated studies in this field. Spomer (39) has shown, for example, that the temperature optimum for initial growth and development of *Geum turbinatum* is high (up to 27° C), but that extended growth occurred best and plants in chambers most closely resembled those in the field when day temperatures were about 12 to 14° C. Plants could be forced into dormancy by average daily temperatures of less than 8° C but not by short photoperiods. This remains an interesting problem, since average

temperatures in the field are never as low as this when the plants begin to exhibit unmistakable signs of dormancy. In the field, flower primordia form during the summer and require the low temperatures of winter for subsequent development the following spring. No manipulations of temperature or photoperiod in the growth chamber, however, would result in flower primordia formation, although in some experiments this could be induced by ultraviolet light.

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