

# CHAPTER 4-5

## ADAPTIVE STRATEGIES: GROWTH AND LIFE FORMS

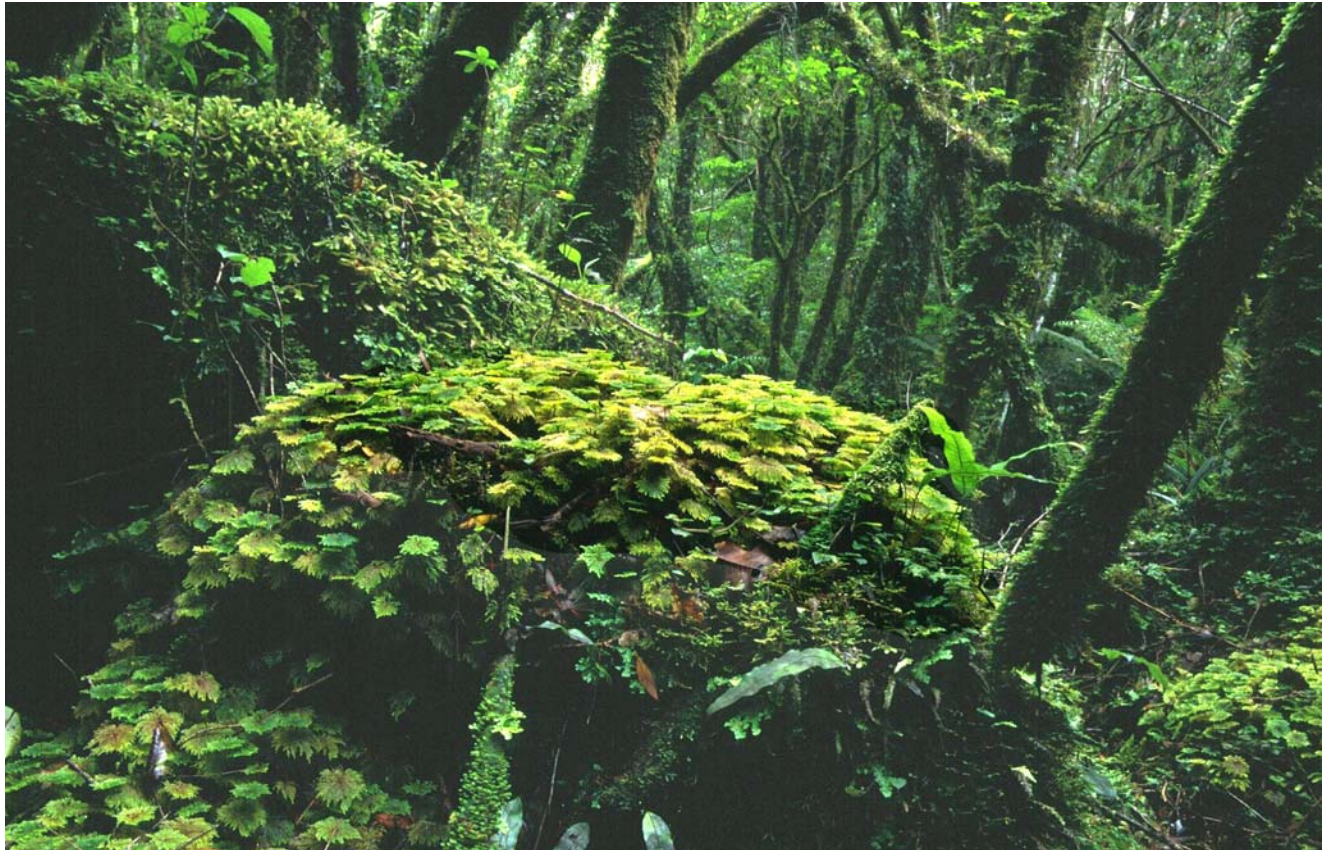


Figure 1. *Hypnodendron menziesii* demonstrating the clonal growth and dendroid growth form that is possible in a humid climate such as that in New Zealand. Photo by Jan-Peter Frahm.

### Growth Forms and Life Forms

Bates (1998) concluded that life form is a useful concept in bryophyte ecology because of the "exceptionally high dependence of bryophytes on transient external water supplies." He points out that for bryophytes it is not the individual that forms the ecological unit, but rather the clonal or colonial life form (Figure 1). The life form is so constructed as to minimize evaporative loss while maximizing photosynthetic light capture. In the Taymyr Peninsula, Siberia, differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions (Vilde 1991).

### Definitions

Meusel (1935) describes **growth form** as the overall character of a plant and explains it can only be determined by detailed morphological analysis. It is a purely morphological term, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and

assemblage of individuals (Warming 1896; Mägdefrau 1982). Life form embodies all the selection pressures that are brought to bear upon a species, or in the words of Mägdefrau (1969), "the organization of a plant in correspondence with its life conditions."

If these life forms persist genetically, we tend to assume they have adaptive significance. Gould and Lewontin (1979) and Mishler (1988) warn us of the trap of this type of thinking. We must recall that selection works against those things that are not beneficial, and that it is a slow process, even slower for those things that convey only a slight disadvantage. Furthermore, such characteristics as life forms may simply carry an occasional advantage, an occasional disadvantage, or little difference from another life form. Correlation of life form with habitat, however, can be used as supporting evidence for the adaptive value of a given life form.

Early classification of life forms had little relevance for bryophytes. Dansereau (1957, in Ricklefs 1990) classified plant life forms into trees, shrubs, herbs, epiphytes, lianas (vines), deciduous, evergreen, and bryoids. Raunkiaer (1934) relied primarily on winter characteristics and based his system on bud position:

**phanerophytes** (*phanero* = visible) – tips of branches; moist, warm environments

**chamaephytes** (*chamae* = dwarf) – shrubs and herbs, buds near soil; cool, dry climates

**hemicyptophytes** (*hemicypto* = half hidden) – die back to ground in winter; cold, moist

**cryptophytes** (*crypto* = hidden) – buds buried by soil; cold, moist

**therophytes** (*thero* = summer) – seeds; deserts, grassland

## Jargon of Life History

First, perhaps it is necessary to distinguish between **life history** (or life cycle) traits and **life forms**. As During (1979) points out, **holomorphy** (total form, Hennig 1966; the German *Gestalt*) of plants resulting from their adaptations to their environments certainly relates to their strategies. However, the **life strategy** refers to life cycle characteristics and their timing (treated in the next chapter), whereas **life form** refers to the morphological characters of individuals as well. La Farge-England (1996) points out the inconsistencies in the literature regarding the term **life form** and supports Barkman (1979) by defining it as "the overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment." **Growth form**, she reminds us, is "the structural architecture of the individual moss plant." But such architectures can be modified by the environment, hence merging life form and growth form (Tangney 1998). It would seem simpler to define one as the genetically programmed form and one as the environmentally modified form, but the muddle in the literature has crossed those lines with both terms. Thus, even with the foregoing definitions, confusion in the use of terms will still be with us and I shall make little attempt to unravel their use in the literature presented here. Therefore, interpretation of their use should be done with caution.

## Growth Forms

Since growth form is the simpler result of genetics, we should examine that first. As La Farge-England (1996) stated, the terminology of growth form, branching pattern, and position of perichaetia have been used inconsistently in the literature. This morass of literature makes it difficult to compare studies and to sort out the real meanings in nomenclature. After an extensive review of the literature and usage of the terminology, she recommended the following interpretations:

1. **Growth form** is distinct from **life form**.
2. Direction of growth does not necessarily imply perichaetial position; some **acrocarpous** mosses (having terminal perichaetia) grow horizontally, whereas some **pleurocarpous** ones (having perichaetia in lateral buds or on short side branches) grow erect.
3. **Cladocarpus** (Figure 2) is distinct from pleurocarpy, with perichaetia terminal on lateral branches and with

juvenile leaf development similar to that on vegetative branches; perichaetial branches have lateral primordia that potentially develop subperichaetial branches. (It is defined in *Glossarium Polyglottum Bryologiae* as a type of pleurocarpy having sporophytes borne terminally on short lateral branches, as in *Fontinalis*).

4. **Pleurocarpy** is defined as having perichaetia terminal on lateral innovations that appear sessile and swollen along supporting axes. Juvenile leaves are morphologically different from those of vegetative branches. Perichaetial innovations lack lateral branch primordia and thus do not produce subperichaetial branches. Pleurocarpy is restricted to Hypnales, Hookeriales, and Leucodontales, including Spiridontaceae and Racopilaceae.



Figure 2. Cladocarpous branches of *Macromitrium microstomum*. Photo by Janice Glime.

But traditionally, growth forms of mosses have been divided into those that are **acrocarpous** (Figure 3) and stand vertically (**orthotropic mosses**) and those that are **pleurocarpous** and lie horizontally relative to the substrate (**plagiotropic mosses**; Figure 4) (Meusel 1935). This of course leaves a few out of the scheme, as noted by La Farge-England. The orthotropic mosses can be further divided into the **protonema mosses** (Figure 5), with short or non-existent shoots that wither after the sporophyte is produced, and **turf mosses**, with upright shoots that bear new shoots after the sporophyte forms and subsequently bear further archegonia and more sporophytes; these new growths are the **innovations**. The plagiotropic mosses (Figure 4) include **thread mosses** (e.g. Leskeaceae, some Amblystegiaceae), with little difference between the main stem and lateral branches, the **comb mosses** (e.g. Hypnaceae, Brachytheciaceae, Meteoriaceae), with a strong main shoot with many simple or branched lateral branches, and the **creeping-shoot mosses** (e.g. *Leucodon*, *Antitrichia*, Climaciaceae, Hypnodendraceae), with rhizomatous main shoots that give rise to upright main shoots.



Figure 3. Acrocarpous growth form exhibited by *Oncophorus wahlenbergii*. Photo by Michael Lüth.



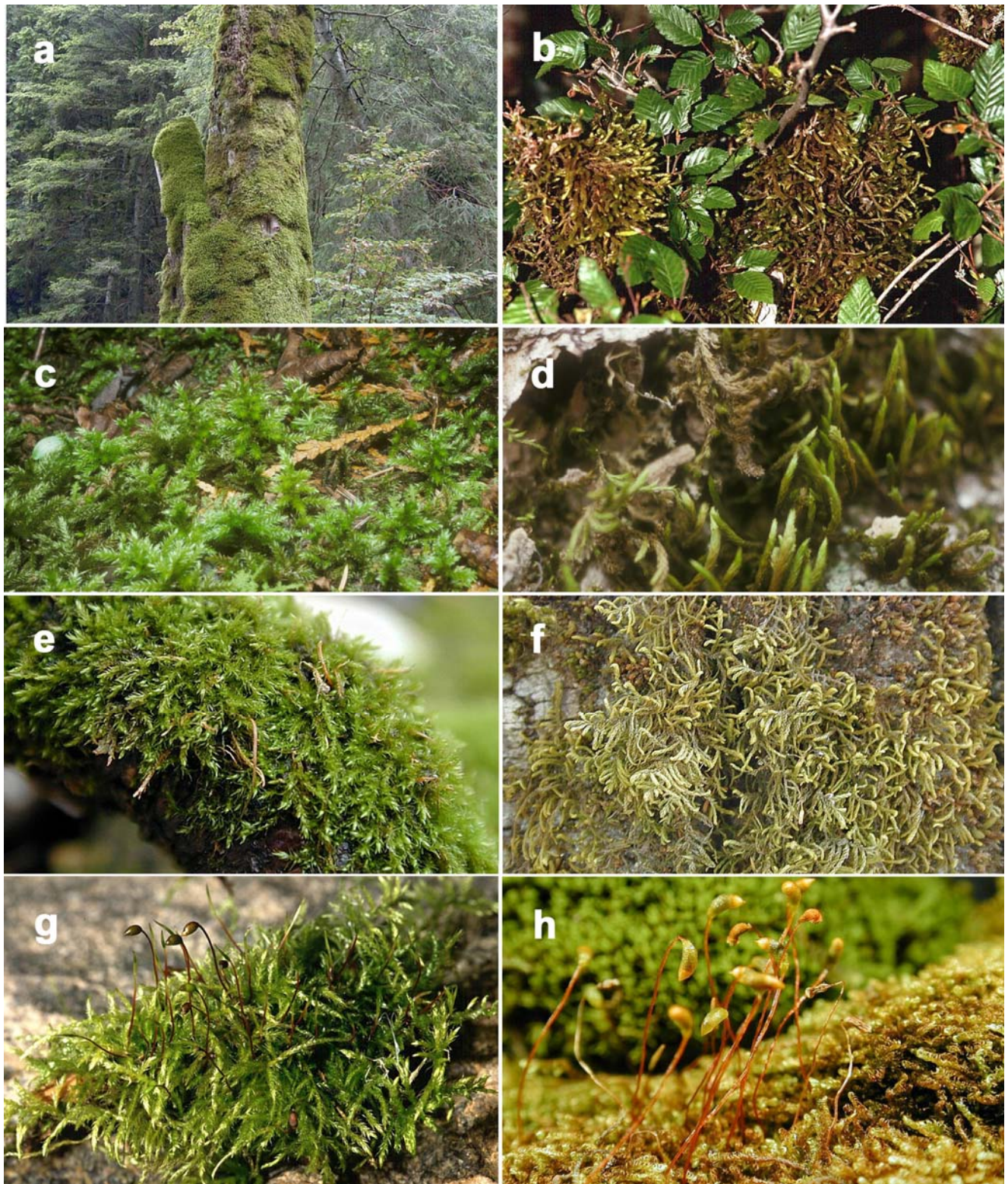


Figure 4. Plagiotropic, pleurocarpous, perennial mosses. **a & b.** creeping shoot mosses – *Antitrichia curtispindula*. **c.** creeping shoot moss – *Climacium dendroides*. **d.** creeping shoot moss – *Leucodon brachypus* var. *andrewsianus*. **e.** thread moss – *Amblystegium serpens*. **f.** thread moss – *Leskea polycarpa*. **g.** comb moss – *Brachythecium reflexum*. **h.** comb moss – *Hypnum sauteri*. **a, b, e-g** photos by Michael Lüth; **c, d** photos by Janice Glime.





Figure 5. Protonema mosses. **Upper:** *Pogonatum aloides*. **Lower:** *Buxbaumia aphylla*. Photos by Michael Lüth.

The same species may exhibit more than one growth form. For example, in some populations *Hylocomium splendens* (Figure 6) exhibits **monopodial growth** (single central axis with apical growth) (Ross *et al.* 1998, 2001). However, some populations can continue by **sympodial growth** (growth produced by lateral buds just behind apex). In forest habitats of temperate to mid-arctic regions the growth is primarily sympodial, creating the stair-step form that easily delineates annual growth (Ross *et al.* 2001). Higher nutrient availability promoted sympodial growth. In tundra and high arctic habitats, monopodial growth predominates and increments cannot easily be discerned. Transplant experiments demonstrated that these traits were plastic, but that natural variability was greater among those shoots in natural populations at transplant sites, indicating a genetic component as well as an environmental component to the differences, affecting both growth and life forms.



Figure 6. Weft life form of *Hylocomium splendens*. Photo by Michael Lüth.

Ross *et al.* (1998) found that the sympodial *Hylocomium splendens* plants had increasing stiffness with stem segment age and flexibility decreased with age up through four years, then declined. However, monopodial plants showed neither of these age effects and no increase in stem diameter with age. The sympodial stems had significantly more cellulose than their monopodial counterparts, providing them with a higher stress yield. The predominance of these two forms differs with habitat, with more northern populations lacking the sympodial branching that defines the annual increments. Økland (2000) further determined that reproductive capacity differs with stem position and age. The apical tips are subject to greater exposure and are less likely to have successful reproduction. Reproductive failure is greatest for older segments buried within the weft (44%), lowest for intermediate vertical positions (12%), and relatively high for the emergent segments. The greatest annual increment is likewise at this intermediate level (2-10 mm below the bryophyte surface) where there is still sufficient light but the loss of water is minimized.

Økland (2000) pointed out the importance of "growth form" in the way that pleurocarpous and acrocarpous bryophytes interact in competition. In our study on Isle Royale (Raeymaekers, Zhang, & Glime unpubl), the interaction between the acrocarpous *Dicranum polysetum* and the pleurocarpous *Pleurozium schreberi* (Figure 7) differed from year to year, most likely depending on the precipitation patterns. In some years, *D. polysetum* increased in area and overran *P. schreberi*, but in other years the reverse occurred. Økland suggested that the relationship of upper segments to lower ones represented **amensalism**, where the lower segments were harmed. Small segments were more easily buried. This relationship can play an important role in both infraspecific and interspecific interactions among bryophytes.



Figure 7. *Pleurozium schreberi* competing with *Dicranum polysetum*. Photo by Herschel Horton.



## Life Forms

Literature on life forms and growth forms is confusing because different authors have used the terms in different ways, sometimes in reverse of the descriptions above. Even in the long-studied tracheophytes, the terms have often been used as if they are interchangeable. In studying loblolly pine trees, Haney *et al.* (1993) illustrated effects of density on "growth form" of loblolly pine tree shape. They found that in low densities, trees were shorter and had more branches. At medium density, they were taller, but branches were few in number. At high densities, trees were tallest and branches were still few (Figure 8). These environmental influences on tree form fit the more encompassing definition of life form described above by La Farge-England (1996). As expected, allocation of biomass changes relative to density (Table 1), resulting in a different form. Such mosses as *Sphagnum* and *Climacium* would be interesting tests of a similar form change in bryophytes. *Climacium* is known to change form, but it appears to be under both environmental and genetic control; effect of crowding was not studied (Shaw 1987).

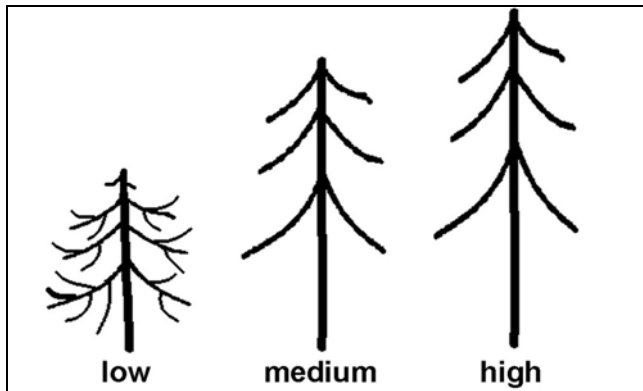


Figure 8. Illustration of forms in loblolly pine at different densities. Based on Haney *et al.* (1993).

Table 1. Allocation of biomass in trees of loblolly pine at three density levels (Haney *et al.* 1993).

	low	medium	high
diameter (cm)	11.87	7.79	6.67
number of whorls	18	11	9
biomass (kg)	12	6.5	4.9
crown ratio	0.79	0.52	0.44
branches	50	27	21
branch length (m)	1.5	1.05	0.9

Bates (1998) raised the question "Is 'life-form' a useful concept in bryophyte ecology?" When he pointed out that most bryophytes are either clonal or colonial, he emphasized that it is these, not individual shoots, that are the functional units. The life form maximizes productivity and minimizes water loss, but it may also function to prevent photoinhibition or scavenge cloud water. Despite its usefulness in indicating moisture and light conditions, Bates considers life form to have limited use "as a framework in ecological studies." He also considers a major problem to be the inconsistent way the concept has been applied in the literature. Life forms also change, as pointed out by Warming (1896). Bates suggested that one interpretation of life form is to consider highly productive

horizontal growth forms like that of *Brachythecium rutabulum* (Figure 9) to be an adaptation for **foraging** (horizontal growth that permits mosses to take wider advantage of nutrients and light; Bates 1998). Life forms do not evolve independently and are closely tied to the life cycle and reproductive traits. Nevertheless, Bates concluded that the concept was useful because of "the high dependence of bryophytes on external transient water supplies." However, the description of life form alone will provide insufficient understanding and will depend on knowledge of its relationship to other attributes of the life strategy.



Figure 9. Horizontal growth form of *Brachythecium rutabulum* that may be used for light scavenging (foraging). Photo by Michael Lüth.

Age changes the life form and its effect on the physiology of *Grimmia pulvinata* (Figure 10) in a different way (Zotz *et al.* 2000). As discussed in the structural adaptations related to water, this moss forms cushions. As the cushion volume increases, so does the water volume. However, the surface area increases two-dimensionally as the volume increases three-dimensionally, causing a decrease in the surface area to volume ratio. This greatly enhances the water retention of the cushion as it enlarges. On the other hand, the CO<sub>2</sub> exchange decreased with size, again because of the reduced surface area. Lowered CO<sub>2</sub> exchange corresponded with lower rates of both net photosynthesis and dark respiration.



Figure 10. Cushion life form of *Grimmia pulvinata*. Photo by Des Callahan.

Nevertheless, life forms are often indistinct from growth forms. A plant is predisposed to a certain growth form, and despite neighbors or environmental conditions, it retains that growth form as part of its life form. In this sense, Mägdefrau (1982) lists ten life forms for bryophytes (Figure 11, Figure 12), to which I (Glime 1968) have added **streamer**.

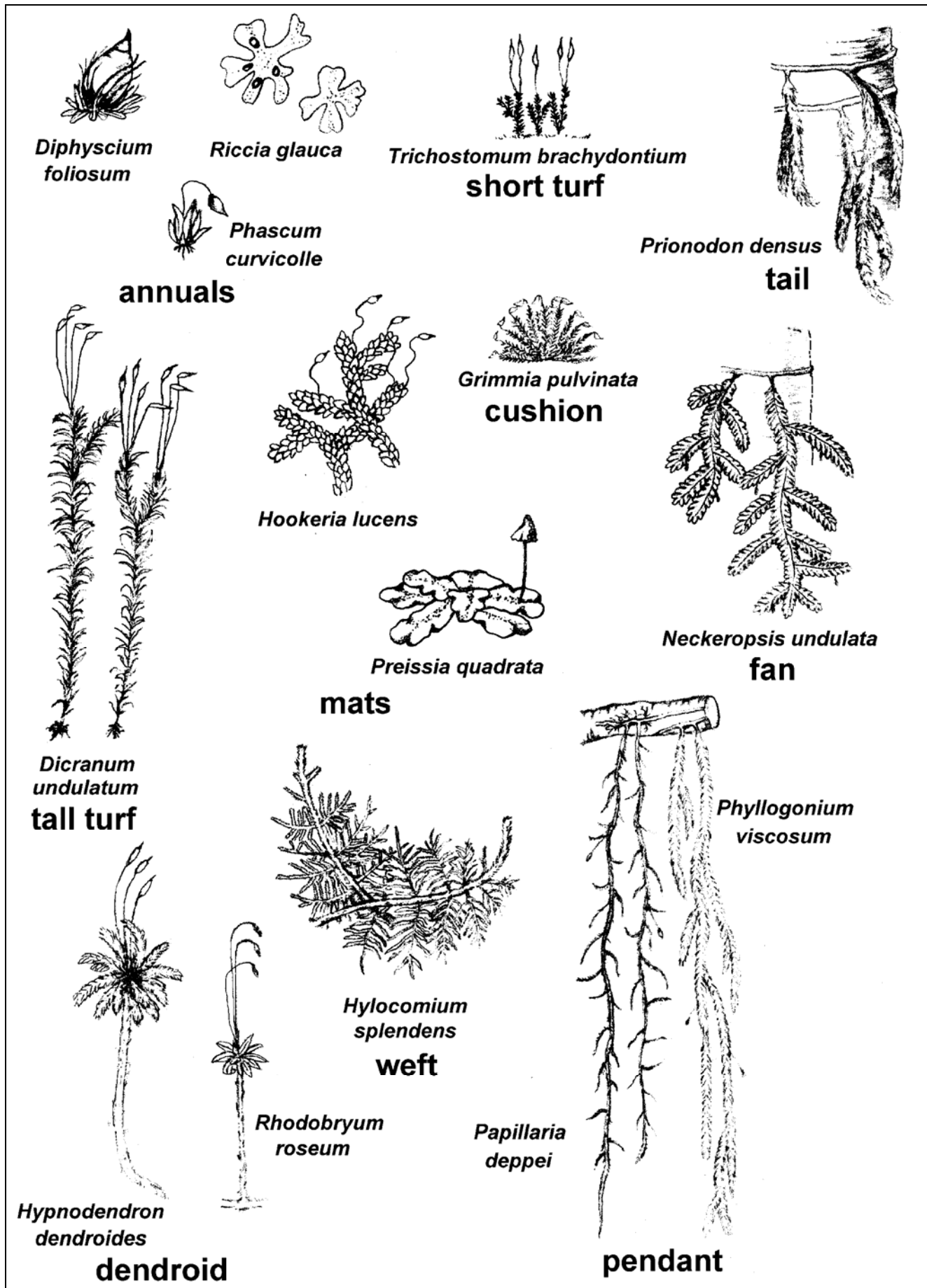


Figure 11. Life forms of mosses and liverworts, based on Mägdefrau (1969). Redrawn by Margaret Minahan.



## Life Forms



Figure 12. Life forms of bryophytes. **a.** Annual – *Ephemerum minutissimum*. **b.** Short turf – *Barbula unguiculata*. **c.** Tall turf – *Polytrichum formosum*. **d.** Mat – *Plagiothecium curvifolium*. **e.** Pendant – *Meteorium*. **f.** Fan – *Neckera urnigera*. **g.** Dendroid – *Pleuroziopsis ruthenica*. **h.** Streamer – *Fontinalis antipyretica*. Photos by Michael Lüth; e & g by Janice Glime.



### Mägdefrau Life Forms

**Annuals** – pioneers; no vegetative shoots remain to carry on a second year; *Buxbaumia* (Figure 5), *Diphyscium*, *Ephemerum* (Figure 12a), *Phascum*, *Riccia*

**Short turfs** – open mineral soils and rocks; regenerative shoots; form spreading turfs for only a few years; *Barbula* (Figure 12b), *Ceratodon*, *Didymodon*, *Marsupella*

**Tall Turfs** – forest floors in temperate zones; can conduct water internally; very tall; persist by regenerative shoots; Bartramiaceae, Dicranaceae, Polytrichaceae (Figure 12c), *Drepanocladus*, *Herbertus*, *Sphagnum*, *Tomenthypnum*

**Cushions** – rocks, bark, Arctic, Antarctic, alpine; usually high light; grow upward and sideways; hemispherical; persistent for many years; *Andreaea*, *Grimmia*, *Leucobryum* (Figure 13), *Orthotrichum*, *Plagiopus*, no liverworts

**Mats** – rocks, bark, [on leaves (epiphyllous) in tropics]; plagiotropic and persistent for a number of years; Lejeuneaceae, most Marchantiaceae, *Homalothecium*, *Lophocolea*, *Plagiothecium* (Figure 12d), *Radula*

**Wefts** – forest floor of temperate zone; hold considerable capillary water; grow loosely and easy to remove from substrate; new layer grows each year; Brachytheciaceae, Hylocomiaceae (Figure 6), *Bazzania*, *Ptilidium*, *Thuidium*, *Trichocolea*

**Pendants** – epiphytes, especially in tropical cloud forests; long main stem with short side branches; Meteoriaceae (Figure 12e), Phyllogoniaceae, some tropical *Frullania*

**Tails** – on trees and rocks, shade-loving; radially leafed, creeping, shoots stand away from substrate; *Cyathophorum*, *Leucodon* (Figure 4d), *Spiridens*, some tropical *Plagiochila*

**Fans** – on vertical substrate, usually where there is lots of rain; creeping, with branches in one plane and leaves usually flat; Neckeraceae (Figure 12f), Pterobryaceae, *Thamnobryum*, some *Plagiochila*

**Dendroids** – on ground, usually moist; main stem with tuft of branches at top; *Climacium*, *Hypnodendron*, *Hypopterygium*, *Leucolepis*, *Pleuroziopsis* (Figure 12g), *Symphogyna hymenophyllum*

**Streamer** – long, floating stems in streams and lakes; *Fontinalis* (Figure 12h)

### Environmental Influences on Life Form

These eleven forms may be further divided, as suggested by Horikawa and Ando (1952). As Mägdefrau (1982) points out, light and water are the predominant influences on life forms. Crowded shoots with dense foliage facilitate water movement and retention in areas with sufficient soil water, thus favoring **tall turfs**. **Mats**, **wefts**, **tails**, and **fans**, on the other hand, are unable to obtain water by capillary action, but depend on the capillary spaces to retain water and extend their periods of activity. **Pendants** (Figure 12e) are like laundry on the clothesline and are particularly susceptible to drying; hence they live in places with considerable rainfall or fog, assumedly directing the water to the growing tip. Mägdefrau (1982) cites his observations on mosses near waterfalls to support this assumption.

The **cushion** life form (Figure 13) is highly adapted for water conservation. Proctor (1980) found that the laminar flow patterns over moss cushions were consistent with the measured loss of water from surfaces of varying degrees of roughness. Water loss increased rapidly beyond a critical wind speed, at which the surface irregularities of the cushion could be related to boundary-layer thickness. The thickness of this boundary layer determines the rate of

water loss, with thick layers reducing evaporation. Even cushions have turbulent flow as opposed to laminar flow (Rice *et al.* 2001), and the more deeply the air penetrates into the moss canopy, the more turbulent that flow and the greater the evaporation. Among the growth forms, we would expect cushions to have the least turbulence, with wefts and turfs creating more (Figure 14). Surface roughness increases conductance (Rice *et al.* 2001). However, Proctor (1980) found that hair-points of the leaves that project above the cushion surface reduce boundary layer conductance, for example, by about 20-35% in *Syntrichia intermedia* and *Grimmia pulvinata* (Figure 10), hence serving as an adaptation to reduce water loss.



Figure 13. Cushions of *Leucobryum glaucum* in a mixed hardwood forest in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

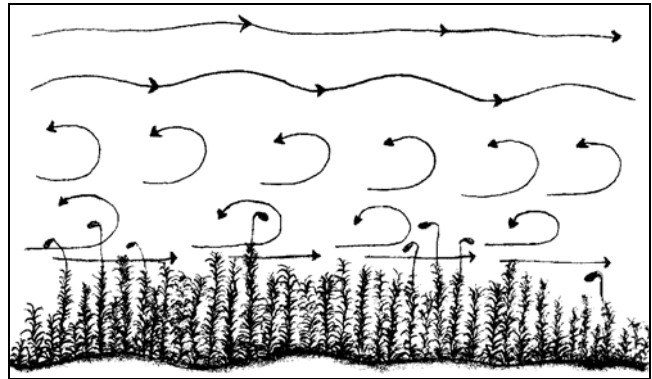


Figure 14. Diagram indicating turbulence and boundary layer as might be found above the irregular surface of a moss weft. Having all stems at the same height, as in a cushion, would reduce the turbulence. Drawing by Margaret Minahan.

Rice *et al.* (2001) have used wind tunnel experiments to examine effects of architectural features on boundary layer thickness and subsequent water balance of bryophytes. Using evaporation rates of ethanol, they were able to assess differences among 11 taxa having a variety of canopy structures. They accounted for 91% of mass transfer of water loss using models based on surface structure. Even the seemingly smooth surface of cushions behaved as turbulent flow rather than laminar flow



boundary layers. Conductance increased with surface roughness, causing those species with greater roughness to have higher conductance rates at all wind speeds.

Water-holding capacity is often more important than obtaining water. In the Antarctic, dense rhizoids contribute to high water-holding capacity in *Bryum algens* (Lewis Smith 1988). In *Schistidium antarcticum* (Figure 15), the **turf** form has a high water-holding capacity, whereas the densely packed **cushion** form has a lower water content relative to its dry weight. Nevertheless, the rate of water loss is much more rapid in the turf form (Lewis Smith 1988). I am puzzled, however, by the more rapid water loss in the more tomentose form of *Bryum algens* than in the form with fewer rhizoids. I would have to conclude that water was held loosely among the rhizoids, contributing to the magnitude of weight loss, and was lost more easily, giving a higher percentage loss. A similar phenomenon could explain the differences between the water loss of the turf and cushion. Lewis Smith found that the reverse relationship holds if the water loss is expressed relative to the initial water content instead of the dry weight, supporting my interpretation.



Figure 15. Cushions of *Schistidium antarcticum* on Macquarie Island in the Antarctic. Photo by Rod Seppelt.

Physical factors of the environment also contribute to life form in other ways. Once the growing apex reaches the surface of the **cushion** or exceeds the protection of a rock, it would be exposed to air movement where it would dry out. However, the ethylene concentration around the growing tip would also diminish. Whenever the moss slowed its growth and fell below its fellow cushion members, the higher ethylene concentration trapped within the cushion could again accelerate its cell elongation. Results with *Fontinalis squamosa* suggest that ethylene in mosses reduces cell division but permits and perhaps enhances cell elongation (Glime & Rohwer 1983). If it indeed acts this way, such a mechanism could be a sensitive and effective control mechanism that would maintain the cushion growth form necessary for maximum moisture retention (Kellomaki *et al.* 1978) and surface light. If, however, ethylene retards elongation as it does in most tracheophytes (Abeles 1973), **IAA** (indole acetic acid, a growth hormone) is probably the controlling factor. IAA is destroyed by light (Goodwin & Mercer 1983), so those branches getting more light would grow less, not to mention being retarded by desiccation, whereas those within the mat would be shaded and grow more, as an etiolation response. Mosses kept humid in a plastic bag in

a place where little light reaches them produce narrow, etiolated shoots. In a terrarium, *Dicranum scoparium*, *Pleurozium schreberi*, and *Brachythecium* all produce etiolated tips, presumably in response to low light (pers. obs.).

Plants, including bryophytes, have specific mechanisms to combat light intensity changes. Species from open habitats respond to simulated shade with a large increase in stem elongation (Morgan & Smith 1981). This increase would carry the plant upward until it topped its competitors and could receive the needed sunlight. Lignified woodland species react much less or not at all; here the futile attempt to top the canopy would result in tremendous amounts of wasted energy. **Cushion** bryophytes, however, respond to shading by each other like species from open habitats. In nature we see rounded cushions of *Leucobryum* and *Dicranum*, and we must wonder if the tall center plants and short border plants are merely a function of age. Yet when a clump is backed up against a rock, it is not as short on the rock side as it is on the other side, but rather it tapers down and away from the rock. Is it light intensity acting on IAA, exposure to desiccation, or ethylene concentration that maintains these cushions, or some combination of these?

In mangrove swamps, Yamaguchi and coworkers (1990) found that small, **appressed** liverworts, especially Lejeuneaceae and Frullaniaceae, predominated, whereas in more landward sites the larger **ascending** taxa such as *Plagiochila* and pleurocarpous mosses were found. This distribution seems counter-intuitive unless the seaward sites were more subject to wind desiccation from buildup across the water, whereas the more landward ones were protected by the forest. Salt tolerance may enter the relationship as well, but this has not been explored.

Birse (1957) showed that a normally monopodial dendroid *Climacium dendroides* can be induced to grow horizontally as a stolon when affixed to a substrate and supplied with ample moisture. It furthermore will reverse its direction of growth if turned upside down, yet, if placed in a moist pot, it will follow the substrate, growing down on the outside of the pot and ignoring gravity. If buried in sand, it will regenerate shoots that Birse *et al.* (1957) observed to grow up to the surface, then grow horizontally. She likewise observed that *Thamnobryum alopecurum* exhibited growth forms ranging from simple branches in dripping water to highly dendroid in very moist air.

Aquatic mosses such as *Fontinalis* do not fall easily into the above classification system. While most *Fontinalis* species hang in a pendant form similar to pendant epiphytes, their physiological relationship to their environment as a result of this growth form is quite different. The tip, instead of receiving water dripping down from the remainder of the plant, is immersed most of the year. This long form, which I have termed **streamer** (Glime 1968; Jenkins & Proctor 1985) is more likely a result than an adaptation. The persistent growth of this moss permits it to grow farther and farther from its substrate, but many branches stack upon each other to make a thick weft, but one that is not easy to remove from the substrate. In *Fontinalis dalecarlica*, rhizoids are generally restricted to bases of stems, and the long, persistent stems are extremely strong (Glime 1980). In *F. novae-angliae*, rhizoids originate throughout the stems,



making a firmer attachment to the substrate. It would be interesting to examine competition in these two taxa since they can occupy the same streams and even the same rocks.

Although many studies describe dominant life forms, these descriptions are rarely based on quantitative data. Kürschner (1994) used mean cover values to describe life forms on basic rocks in nine communities in southern Germany on the northern border of the Schwabische Alb. He found that communities subject to high light and temperature (photophytic and thermophytic) were dominated by cushions, short turfs, and perennial and short-lived colonists (life strategies discussed in the next chapter). As these graded into shady habitats, wefts and mats were more common, with perennial shuttle and perennial stayer life cycle strategies; reproduction was more "passive." Low light species (sciophytes) and aquatic species were perennial fan-formers with sexual reproduction.

## Physical Effects on Growth Form

### Moss Balls

The strange phenomenon of moss balls was reported in 1912 by Dixon, who referred to them as "mosses growing unattached." Bryologists still remain fascinated by these strange organisms that grow in a ball and are mobile, so that at different times any part of the sphere may be exposed to sunlight or substrate. But bryologists are not the only ones fascinated by them. In Japan, a monument is dedicated to their preservation (Iwatsuki 1977).

In 1874, the United States sent an expedition to the Kerguelen Islands in the South Indian Ocean to observe the transit of Venus (Mägdefrau 1987). The surgeon of the expedition was also an amateur botanist and an avid collector. He brought back a "curious moss" that seemed "not to be rooted to another plant, but to be blown about by the wind indiscriminately," as described by the bryologist Th. P. James. Schimper later described these same mosses as having a size that varies between that of a cherry and a middle-sized potato. The smaller balls were *Blindia aschistodontoides*, and the larger ones were formed by stems of *Andreaea parallela* by radiating from a central core of soil or a small pebble. Since then similar wind-formed balls have been found in Alaska, Iceland, Norway, on Mount Ontaka in Japan, and even at the high elevation tropics of Mount Kenya, Mt. Elgon, and Mt. Kilimanjaro in Africa.

Such balls in Arctic and alpine areas could result from **solifluction**. **Solifluction** is a slow creeping of fragmented material down a slope over impermeable material, due to the viscous flow of water-saturated soil and other surficial materials, particularly in regions underlain by frozen ground (not necessarily permafrost) acting as a barrier to downward water percolation. Its drift typically occurs at a rate of 1-10 cm per year (White 2001) in relatively cold regions when the brief warmth of summer thaws only the upper meter or two of loose earth materials above solid rock, which becomes waterlogged because the underlying ground remains frozen and therefore the water cannot drain down into it. Mosses could travel and tumble with it.

Hedberg (1964) interpreted the African balls (*Grimmia ovalis*; Mägdefrau 1987) to form as a result of solifluction. Mägdefrau (1987) tested this hypothesis by experimenting with balls in Teleki Valley of Mount Kenya at 4200 m.

The balls were marked and their locations sketched. When it was dry, there was no solifluction and the moss balls remained in place. However, when they experienced daily watering and frost at night, the balls rotated but held their positions. Rather, it appears that when ice crystals and ice needles form at night, they cause the mosses to be forced away from their substrate and broken off. These freed mosses are blown about continuously and thus grow in all directions, forming balls.

Mägdefrau (1987) observed that none of the mosses in balls had sporophytes, whereas those of the same species growing attached had plentiful sporophytes. He concluded that the growth of sporophytes is prevented by the rolling movement. It would seem likely that young setae and perhaps even archegonia at apices may be damaged by abrasion as they get beaten around over the rocky surface. When mosses lie for a longer period of time on one side, sporophytes develop on the edge of the disk.

On frozen Icelandic soil (Mägdefrau 1982) and Alaskan glaciers (Shacklette 1966; Heusser 1972; Iwatsuki 1976), dislodged mosses blow about across the surface, forming similar balls. During (1992) observes that this life form, which also includes lichen species, results in areas that have high winds and little vegetation.

Perez (1991) attributes the transport of *Grimmia longirostris* moss balls in the Paramo de Piedras Blancas of the Venezuelan Andes to needle ice activity. These balls had a high organic content (19%) and a collection of fine mineral grains (69%), a much higher fine grain than in the underlying mineral soils. This combination of organic content and fine grains affords the moss balls a much higher water retention capability than paramo soil, with water-holding capacity increasing with the size of the ball.

Wind and ice are not the only sources of creating moss balls. Action of waves can create similar assemblages (Figure 17). These strange assemblages of individuals have been reported from as distant places as Alaska (Iwatsuki 1976), Finland (Luther 1979), Japan (Iwatsuki 1956, 1977; Iwatsuki *et al.* 1983), and South America (Eyerdam 1967). Eyerdam found *Fontinalis* in balls up to 15 cm in diameter!

In shallow water near lake shores in Hokkaido, Japan, *Drepanocladus* (*Warnstorfia*) *fluitans* (Figure 16) attaches to small rocks (Iwatsuki 1956); once the rock is dislodged, wave action rolls the moss back and forth, causing it to lie first in one position, then another, with any protruding branches being broken off (Iwatsuki *et al.* 1983). These growths become extremely dense. As the mosses reach shallower water, wave action is even greater. Ultimately they may be deposited in great numbers along the beaches. Stress causes the production of ethylene, and ethylene can result in short, wide cells under stress conditions in higher plants (Abeles 1973). This could partly explain the short, but firm, branches in the moss balls.



Figure 16. *Drepanocladus* (*Warnstorfia*) *fluitans* growing normally. Photos by Michael Lüth.





Figure 17. Moss balls of *Drepanocladus* (*Warnstorfia*) *fluitans* var. *kutcharokensis* of Lake Kutcharo, Japan. **Top:** Moss balls being made by wave action. **Second:** Row of moss balls along shore. **Third:** Moss ball with arrows indicating green, growing apices. **Bottom:** Side branch typical of many of the stems in these balls, creating the dense structure that makes the ball. Photos by Janice Glime; bottom photo by Zen Iwatsuki.

Even animals can create moss balls. In the Dutch wetland forest, it is foraging pheasants that turn the mosses upside down and initiate the upward growth that creates the ball (Wiegiers 1983). Although *Dicranum scoparium* and

*Mnium hornum* formed such balls, other upturned wetland taxa did not.

### Adaptive Significance

Often the life form is a passive response to exposure; any protruding individual is more subject to desiccation and hence has a shorter period in which to be active for photosynthesis, thus reducing its growth rate below that of its shorter but hydrated neighbors. Although this is more commonly known in cushions, Perez (1991) found that the same phenomenon occurs in moss balls of *Grimmia longirostris* in the Venezuelan Andes. This spherical life form holds more water than the soil, and larger balls hold more than small ones. In some cases, the form may be modified to accommodate the capture of cloud water or to avoid photoinhibition.

Mägdefrau (1935) found a clear relationship between life form and type of conduction. Dense tufts increase conduction, but there is considerable humidity difference within the tuft that suggests an important role in water retention (Zacherl 1956). When the air humidity is only 50% a few cm above the tuft, it can be as much as 90% within the tuft. Larger volumes are able to store more water, and volume increases more rapidly than surface area. Larger cushions have a greater volume of water per unit of surface area, thus losing less to evaporation than small cushions with a thinner boundary layer and greater proportion of surface area (Proctor 2000). Zotz *et al.* (2000) used *Grimmia pulvinata* to demonstrate that the greater the size of the cushion, the more resistance it had to water loss. This size increase had no effect on the water-holding capacity on a dry mass basis, and the combination of these two factors contributed significantly to the length of the hydration period.

The cushion growth form (Figure 18) is important in decreasing the loss of water by reducing the turbulence of airflow (Figure 14). At low and even moderate wind speeds, the evaporative water loss from the cushion mimics that of a flat or rounded surface of the same area (Proctor 1984). This form is reminiscent of the tundra formations, where the cushions of seed plants not only impart resistance to moisture loss, but facilitate warming and protect from wind damage. The cushion shape presents a boundary layer that resists loss of moisture and permits wind to cross the plants with a minimum of disruption. Proctor (1979, 1980, 1982) found that the resistance to water loss extends the period of active metabolism after the precipitation stops. Nobuhara (1979) showed that *Bryum argenteum* increased its water-holding capacity as the volume increased, with more than 100 shoots reducing the water loss to something very small.

The wind also can play a role in the formation of the cushion. As a branch, whether moss or tracheophyte, grows above the cushion, drying and wind action slow its growth and may even damage the terminal bud. Proctor (1980) demonstrated that when such surface irregularities reach the thickness of the boundary layer, there is a rapid increase in water loss at higher wind speeds. Thus, when a branch extends beyond the cushion, the other branches can catch up with it in growth before it is able to regain hydration and resume its growth, and if the terminal bud has been damaged, that growth may never occur.





Figure 18. *Leucobryum glaucum* cushions. Photo by Janice Glime.

Lewis Smith (1988) described the ability of dense turfs of *Schistidium antarcticum* (Figure 19) to hold strongly to their water content, but that the less densely packed shoots of cushions in xeric conditions could not maintain as high a water content as the turfs. Longton (1979a, b) drew a similar conclusion, noting that in Antarctica the plant size decreases as the shoot density increases; the shorter, more compact growth form could be adaptive to the cold, relatively dry habitats.



Figure 19. Dense growth of *Schistidium antarcticum* on Macquarie Island in the Antarctic. **Upper:** dense and well-hydrated turf with *Ceratodon purpureus* growing in the crevices. **Lower:** Uneven turf with exposed tops exhibiting dehydration. Photo by Rod Seppelt.

For endohydric mosses, growth form is important in water retention. Longton (1979a) found variations in the seasonal growth patterns of *Hypnum cupressiforme*, and was able to relate these to water supply. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture:

### Relationship of Growth Form to Moisture

#### high moisture

dendroid & thalloid mats

rough mats

smooth mats

short turfs & cushions

low moisture

Birse (1957) found that in some cases the growth form of certain species of bryophytes is almost invariable, whereas in others variation occurs according to the conditions of the habitat. Birse (1958a), reported that as long as there was a constant ground water supply, a variety of growth forms could flourish, especially tall turf and dendroid forms. In the absence of ground-water supply, short turfs, round mats, and one dendroid species (*Climacium dendroides*, Figure 20) were the only forms to survive.

Dendroid mosses would seem to be particularly vulnerable to desiccation, with only a single stem in contact with the substrate and many exposed branches. Lorch (1931) found a correlation between the development of the central strand and the degree of branching, whereas the rhizome central strand became less developed, suggesting a greater importance for aerial water sources over soil sources as branching increased. Trachtenberg and Zamski (1979) supported these findings, re-affirming the importance of water absorption through the whole surface of the gametophyte and the utility of **apoplastic** transport.



Figure 20. *Climacium dendroides*, showing dendroid growth form. Photo by Michael Lüth.

Sollows and coworkers (2001) concluded that the colonial growth form of *Bazzania trilobata* (*i.e.* having branches lying on top of other branches; Figure 21) protected at least some inner shoots from the extreme exposures they experienced following clearcutting, avoiding the extinction of net photosynthesis observed in laboratory experiments following dehydration for 1-12 days.

Nakatsubo (1994) compared growth forms in the subalpine region in Japan and found that xeric species were indeed often **large cushions**, as well as **compact mats**. Mesophytic species, on the other hand, comprised **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor. He demonstrated that the evaporative rate per dry mass was indeed much less in the xerophytic cushions and compact mats than in the mesophytic forms. While the evaporative



rate and dry mass were closely correlated with the growth form, the evaporative rate per basal area was not necessarily smaller in xerophytic taxa.

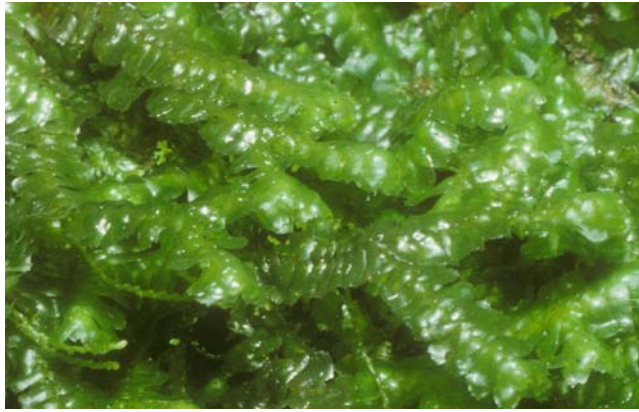


Figure 21. *Bazzania trilobata*, illustrating the overlapping nature of the branches. Photo by Janice Glime.

During (1979) likewise related the growth form to the habitat. He found that *Campylopus flexuosus*, *Orthodicranum montanum*, and several other taxa form large turfs with almost no vegetative reproduction when living in moist, undisturbed environments, but when found in dry forests they consist almost entirely of dense cushions of easily detached branchlets.

But what empirical evidence do we have that the various growth forms and life forms actually afford any moisture advantage? Hanslin and coworkers (2001) demonstrated that increased shoot density of *Dicranum majus* and *Rhytidiadelphus loreus* actually had a negative effect on relative growth rate and green biomass, but that these were optimal at intermediate shoot densities in conditions of low relative humidity. It is likely that these species suffered a trade-off between light availability and moisture advantage at higher densities. In contrast, Bates (1988) found that *Rhytidiadelphus triquetrus*, likewise a boreal moss, had optimal growth when the colonies were most dense (1000 shoots  $\text{dm}^{-2}$ ). Apparently in this case the dense packing of the shoots gives the advantage of reduced water loss and outweighs the disadvantage of reduced irradiance.

## Habitat Relationships

Certain growth forms seem to fare best in certain kinds of habitats (Proctor 1990). In the absence of direct physiological evidence, we can use the observed field relationships to form hypotheses concerning the best life form strategies.

### Deciduous Woodlands

Proctor (1990) suggests that **large size** and **rapid growth** are important for woodland and grassland bryophytes to permit them to grow above the litter and surrounding vegetation. This life form permits them the competitive life strategy. Moist, shady habitats are more favorable for **smooth mats** and **small cushions**, but larger taxa occur as well, taking advantage of nutrients in throughfall and exposing more surface area for photosynthesis. In her study of British deciduous woodlands, Birse (1958b) found that **wefts** and **mats**

predominated, responding primarily to light as a determinant of abundance.

In humid, montane **tropical forests**, **pendant** and **fan** forms provide the most surface area for interception of the limited light without sacrificing moisture in this humid climate (Proctor 1990). Furthermore, they are able to trap water from mist and clouds. However, the great exposure makes them vulnerable to air pollution.

### Pine Woods

Using Proctor's principles as a guideline, then what should we expect in a pine forest where leaf litter is a minimal problem? Seim *et al.* (1955) examined a Jack pine forest (*Pinus banksiana*) in Itasca Park, Minnesota, USA, and found **wefts** and **mats** as the predominant growth forms, with **cushions** and **turfs** comprising most of the remaining taxa. Gimingham and Robertson (1950) likewise found predominately wefts in Northern Britain. However, in another study, Moul and Buell (1955) found the turf type to be predominant (84%) in a sandy coastal pine woods of New Jersey, as did Hamilton (1953) in the hills of central New Jersey, USA. In alpine regions of Japan, Nakatsubo (1994) found that mesophytic species consisted of **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor.

### Epiphytes

Horikawa and Nakanishi (1954) developed a key to the "growth" (actually life) forms of Japanese epiphytic bryophytes. In it they included **small cushion**, **large cushion**, **turf**, **fascicular & shrubby**, **dendroid**, **simple feather**, **branching feather**, **mat**, **carpet**, **hardly pressed mat**, **loosely pressed mat**, **epiphyllous**, **pendulous**. They pointed out that species will vary with growing conditions, causing the same species to be assigned to more than one type.

### Peatlands

Some terrestrial and peatland bryophytes may solve the  $\text{CO}_2$  problem by a cushion or other dense growth form (*e.g.* *Sphagnum*) that provides  $\text{CO}_2$  mostly from their own transpiration stream. In fact, *Sphagnum* seems to take advantage of  $\text{CO}_2$  rising from deep in the peat, bringing up carbon stored there 1000 or more years earlier. Perhaps there is some advantage to having your living parts sitting on top of your dead parts!

### Aquatic

Aquatic mosses such as *Drepanocladus vernicosus* rely on a water medium when submersed but benefit from close contact when emergent (Frahm 1978). Aquatic bryophytes are most constrained by  $\text{CO}_2$ . The **mat** form of *Nardia compressa* and *Scapania undulata* is beneficial in water below  $0.1 \text{ m s}^{-1}$  where its leaf-area index permits it to exploit the low boundary-layer resistance of high velocities without incurring a high drag. On the other hand, the **streamer** form of *Fontinalis* provides the most exposure (maximum surface area) in relatively quiet water of less than  $0.01 \text{ m s}^{-1}$  where boundary-layer resistance is high. Nevertheless, *Fontinalis*, with the same streamer life form, occurs in very rapid and turbulent water of mountain streams. Perhaps the turbulence itself permits enough  $\text{CO}_2$  to mix with the water for the moss to take advantage of its greater surface area.



In the Antarctic, aquatic mosses showed the greatest plasticity when submerged compared to being grown in the air (Priddle 1979). *Calliergon sarmentosum* grew longer stems (longer internodes) and larger leaves in the water, whereas *Sanionia uncinatus* varied little from its terrestrial form.

### Deserts

It is significant that Frahm (1978) found only 9% of the bryophyte flora of the Sahara to be pleurocarpous. In the moist boreal forest, pleurocarpous is the dominant form. Pleurocarpous mosses expose much more surface area to the drying atmosphere; rather, in the dry desert, **small cushions** and **wefts** (loosely interwoven, ascending shoots capable of growing out of the sand are better adapted to the dry and shifting substrate.

### Polar Regions

Longton (1979b, 1982) followed the life forms that Gimingham and Birse (1957) attributed to the polar regions in attempting to compare the Antarctic to other polar areas. He considered four Arctic bryophyte habitats: wetlands, mesic communities, polar deserts, and bryophyte-dominated habitats. He considered wetlands to be dominated by the **tall turf** life form, with lesser representation of **short turfs** such as *Seligeria polaris* on small stones.

Mesic communities had a wider range of life forms than the wetlands, but the **tall turf** was still a dominant, with **short turfs** and **mat-forming** species also among the dominants. Although Longton (1979b) recognized five habitat types among the mesic communities, these forms were generally common among all five mesic communities. However, in Iceland, the **weft** community joined the **tall turf** in prominence, along with mats of leafy liverworts. Furthermore, the birch woods there had abundant weft mosses.

Gimingham and Smith (1971) showed that the *Polytrichum alpestre* and *Polytrichastrum alpinum* turfs lost water more slowly than *Chorisodontium aciphyllum* and *Sanionia uncinatus* in the same habitats, attributing this to the waxy cuticle on the former two. That *P. alpinum* loses only about 10% of its water when centrifuged suggests that most of its water is held internally compared to the 20% lost from *Chorisodontium aciphyllum*.

The dry polar desert fellfields have **cushions** of both mosses and flowering plants, but other open areas have compact forms such as **mats**, **carpets**, and **short turfs** (Longton 1979b).

The bryophyte-dominated communities are those unsuitable for most tracheophytes (Longton 1979b). These include boulders, cliffs, musk ox dung, and hollows where snowmelt is late. The latter supports **large cushions** and **tall turfs** with small flowering plants rooted among them. The **liverwort** *Anthelia juratzkana* (Figure 22) is common here. **Small cushions** form on boulders, cliffs, and other rocky habitats. Rock crevices harbor **small mats** and **turfs**. **Large cushions** form on stony and marshy ground near permanent rivers and streams, with few bryophytes in the streams themselves. Where bryophytes do occupy streams, they are mostly **streamers** and **mats**.



Figure 22. Leafy liverwort, *Anthelia juratzkana*, forming black mounds on the surface. Photo by Michael Lüth.

The most unique of the polar habitats are those enriched with nitrogen by animal dung and support dense communities of dung mosses (Splachnaceae). Bird perches and lemming burrows support short turfs of acrocarpous mosses (Longton 1979b). Soil fractures between the polygons support short turfs of cosmopolitan taxa such as *Bryum argenteum*, *Ceratodon purpureus*, *Funaria hygrometrica*, and *Marchantia polymorpha*.

*Racomitrium lanuginosum* forms extensive heaths resembling very large cushions in areas where it can gain water from the saturated atmosphere (Longton 1979b). In areas with frequent precipitation as well as mist, *Sanionia uncinata* forms moderately thick mats.

In the Antarctic, stones and gravel of nearly level ground support short turfs and cushions (Longton 1979b). In addition to these, calcareous substrata may have mats. Rock crevices have short turfs, small cushions, and mats.

### Alpine

Alpine habitats seem to support mosses that resemble miniature tracheophyte growth forms. Cushions are common, but also carpets cover the dirt and provide protection from erosion. In studying the Ukrainian Carpathian Mountain alpine region, Ulychna (1970) included, in addition to these, bunches, dendroid, and interlacements, the latter two primarily in the transition into forest.

### Studies Needed

While these growth and life form relationships to habitat seem to be well supported by field studies of species present, there has been little attempt to demonstrate that the proposed water relationships actually benefit the bryophytes. Transplant experiments need to be performed that compare the water loss of the various forms in a range of habitats, as well as their survival in this adult form without the need for surviving an establishment stage.



## Summary

**Growth forms** are those genetically controlled characteristics of plants that determine their shape. These are manifest as **acrocarpous** with terminal perichaetia (including **protonema mosses** and **turf mosses**), **pleurocarpous** (**plagiotropic**, including **thread mosses**, **comb mosses**, and **creeping-shoot mosses**) with lateral perichaetia, **cladocarpous** with perichaetia terminal on lateral branches. **Life forms** encompass overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment.

The most widely used classification of **life forms** includes **annuals**, **short turfs**, **tall turfs**, **cushions**, **mats**, **wefts**, **pendants**, **tails**, **fans**, **dendroids**, and **streamers**. These can be subdivided, and a few others may exist in less well known habitats.

Growth forms and life forms of plants can aid in water retention by **reducing air resistance**, **increasing boundary layer thickness**, **providing capillary spaces**, and **protecting each other**. Thalloid forms protect one side of the plant at the expense of the other, but cuticular substances reduce the loss on the exposed side. Open growth forms (e.g. dendroid, rough mat, pendant) are more subject to water loss than compact, tight ones (e.g. smooth mat, short turf, cushion). The **cushion** form is able to provide the least surface exposure per unit of biomass and apparently has the lowest water loss rate. Conduction forms seem to correlate with growth forms, with dense turfs increasing conduction as well as water retention.

**Cushions** and **moss balls** are formed as exposed shoots are broken off by force of wind, abrasion, and desiccation. Moss balls generally have a pebble at the center and arise in areas of wave action, wind on ice, solifluction (possibly), or other physical factors that tumble the moss.

**Deciduous forests** require large size and rapid growth such as wefts and mats to obtain enough light and avoid burial by litter. **Humid forests** support pendants and fans that can get moisture from fog and mist. **Pine forests** have wefts and mats, but also cushions, turfs, and smooth mats. **Epiphytes** include mostly appressed taxa such as smooth mats and small cushions, but a variety of other forms are possible in sufficient moisture. **Peatlands** take advantage of density to conserve moisture. **Aquatic** bryophytes are limited by availability of CO<sub>2</sub> and reduce the boundary layer resistance with **mats** or increase surface area with **streamers**. **Desert** mosses conserve water with small cushions and wefts. **Polar regions** support a variety of forms, depending on the habitat, with cushions predominating in habitats where tracheophytes also form cushions; turfs are common. **Alpine** bryophytes also benefit from the cushion form.

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