Wind-acclimated thallus morphogenesis in a lichen (Evernia prunastri, Parmeliaceae) probably favored by grazing disturbances

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How does the morphogenesis of a widespread epiphytic lichen interact with the environment, leading to amazingly polymorphic and wind-tolerant fruticose thalli? A series of photographs showed that the normal branches were basically even and flat with isotomic-dichotomous branchings. Numerous deviations from this basic regular pattern were found and traced back to their origins in the asymmetry of the branches’ cross sections. This was observed quantitatively (statistically testable) in the field, while the thalli were growing. This large variability in growth of single branches was a prerequisite for the polymorphism seen in complete thallus growth forms. The structure and distribution of the mentioned important asymmetries in branch cross sections can best be explained by the effect of grazing on cortex and phycobiont layer. Very small-scale growth observations and experimental simulation confirmed this. In thalli with many such small-scale variations in branch growth the overall thallus growth form became wind acclimated as a result of the selective effect of wind exposure on the thallus phenotype: branches growing windwardly grew more slowly. Such thalli were well protected from being dislodged by wind, and they desiccated slowly as demonstrated by a previous study.

Key words: ecomorphology; Evernia; growth form; lichenophagy; microclimate; morphogenesis; Parmeliaceae; plant-animal mutualism; variability by disturbance.

Wind-exposed plants face a high risk of desiccation and wind dislodgment. In phanerogams an important way of coping with this problem is the morphogenetic development of wind-acclimated growth forms throughout the individual ontogenesis, as seen in the shape of tree crowns in windy landscapes (Nobel, 1981). (The term “growth form” will be used in order to express the detailed shape—dense, loose, aerodynamic, etc. of a body, not just its basic crustose, foliose, or fruticose form.) Morphogenesis in such phanerogams depends on a highly complicated architecture of different tissues. Lichens completely lack such tissues. Correspondingly, their growth forms are often only two-dimensional, especially on wind-exposed surfaces. Such crustose or foliose growth forms do not exceed the laminar microscale boundary layer covering the substrate (Nobel, 1981) and therefore do not suffer the detrimental effects of turbulent wind. How then can fruticose lichen species successfully develop their tall shrub-like thalli on wind-exposed surfaces in spite of the primitive morphology?

Evernia prunastri (L.) Ach. is the most common of such fruticose lichen species on exposed tree trunks in Europe (Poelt, 1969). The individual branches of E. prunastri grow basically flat and isotomic-dichotomous (Beltman, 1978), but with frequent anisotomies in their (annual) bifurcations (Stone and McCune, 1990) as well as occasional adventive branches on the branch surface (also “lobuli”; Beltman, 1978). Although the morphogenesis mainly consists of only the two-dimensional basic processes, one finds extremely variable, polymorphic growth forms (Beltman, 1978; Wirth, 1980), which seem to correlate to wind exposure, as in phanerogams (Zimmer, 1994). Therefore I investigated three questions: (1) What morphogenetic patterns make the polymorphism of E. prunastri possible? (2) How do these morphogenetic patterns interact with the environment? Important environmental factors on the solitary tree trunks studied are (a) the microclimate of the exposed substrate and (b) grazing by arthropods, which occur in densities of up to 25 animals/thallus and mostly prefer E. prunastri compared to other epiphytic lichens (Prinzing, 1996, 1997; Prinzing and Wirtz, 1997). (3) Do the (combined) effects of these mechanisms influence the ontogenetic development of wind-tolerant growth forms?

Unfortunately, a direct experimental test of the effect of grazing on the phenotypic acclimation of the whole-thallus growth form is hardly feasible: application of insecticides would probably not prevent grazing for a sufficiently long period to affect the very slow growth of branches. The effects of earlier morphogenetic disturbances due to grazing would not be suppressed anyway. Mechanical exclusion of grazers (e.g., by small fences) is problematic, because it would also influence the microclimatic wind exposure. Nor is it possible to exclude all grazers from the whole tree trunk for months or years because they are dispersed by wind (Farrow and Green, 1992) and have a very wide distribution (Prinzing and Wirtz, 1997). Thus, the overall effect of grazing on the shape of the whole thallus can only be inferred from an investigation of the growth patterns behind this effect. The investigation, therefore, focused on the thallus description at all scales from the single feeding trace to the...
complete growth form of the thallus. The respective patterns had to be recognized by eye on photographs of the living thallus in the field (for comparable photographic observations see Stone and McCune [1990]).

MATERIALS AND METHODS

Investigations were conducted at 24 sites, situated in the districts of Rendsburg-Eckernförde and Plön near Kiel (northern Germany, hilly landscape near the Baltic Sea, elevations of <50 m above sea level, oceanic-temperate climate). Average yearly precipitation ranges between 750 and 800 mm (sites 1, 2, 6–18), 700–750 mm (sites 3–5), and 650–700 mm (sites 19–24) (Raabe, 1987). Evernia prunastri was found on trunks of solitary trees situated along avenues in villages (sites 6, 10, 11), or small roads through agricultural landscape (sites 4, 14–19, 21), in hedgerows (sites 7, 20, 24), in clearings (site 1), at forest edges (sites 2, 8, 13, 18), or within meadows or fields (sites 3, 5, 9, 12, 22, 23), mainly on oaks (Quercus robur; sites 1–8, 11, 12, 14, 16–24), lindens (Tilia spp.; sites 4, 6, 10), ash (Fraxinus excelsior; sites 9, 15), and sometimes beeches (Fagus sylvatica; sites 1, 13). On these trunks E. prunastri mostly occurred at heights of 0.4–3.0 m above ground level, mainly on the west or northwest faces. All trees investigated had a circumference of >2 m at a height of 1.5 m.

Thalli were mostly shrub-like, standing out from the trunk up to 20 mm. Branches were 0.5–4.0 mm wide and 0.2–0.5 mm thick. Thalli covered basal surfaces of 35–500 mm² each. On ~25% of the investigated trees all or many of the thalli were densely covered with green algae (Pleurococcus sp.; mainly sites 1, 2, 4, 6, 16). Specimens of E. prunastri v. herinii (Duv.) Maas G., which are characterized by a complete lack of the lichen substance usnic acid (Culberson, 1969; Poelt, 1969), were found at sites 6 and 7.

Observations and experiment—Large-scale photographs were taken (a) in the first year from August to April at intervals of 2–3 mo to document the development of thalli in seven trunk areas (trunk area = area covered by a photograph) on five trees (oaks and two ash trees; sites 15, 17, 23, 24) (scale 1:1.25) and (b) in the second year in January and April (three trunk areas on two oak trees [sites 23, 24], scale 1:2:1). Small-scale photographs (1:2) were taken simultaneously in year 1 from thalli in an additional seven trunk areas.

Five thalli, all strongly overgrown by Pleurococcus algae and located on solitary trees (sites 1, 6), were artificially injured in January. Cortex and phycobiont layers were cut away with a scalpel along two to four rounded edges of branches in each thallus. The thalli were photographed immediately and again after a period of 3 mo. For surgery and photographing (Leitz photo-macroscope M 400, Wetzlar, Germany) three of the thalli were taken into the laboratory for 1 d. They were re-attached using a microscope (Leitz photo-macroscope M 400, Wetzlar, Germany) three of the thalli exactly into the respective gap. The initial orientation of the thalli was restored by fitting the piece of bark (which had been marked in the meantime with colored needles). The single branches was assessed on the large-scale photographs and graphed, sketched, and noted. General elements of “growth form architecture” were deduced later from a comprehensive overview of the documentation.

Thalli or branches that had been detached from bark and fallen off the trunk were collected at seven sites near Kiel in October (15–25 specimens/site; sites 6, 7, 9, 10, 16, 17, 18).

The climatic conditions for thalli on tree trunks were determined according to the following rules: prevailing wind directions at a solitary trunk can be recognized from the shape of surrounding shrubs and tree crowns (“flag trees,” Holroyd, 1970; Noguchi, 1979). Main wind direction is affected by shelter from surrounding hills, hedgerows, and forest edges (Barner, 1983), which are very common in the areas of investigation. The wind exposure below the crown increases with increasing height on the trunk (Kershaw and Larson, 1971). Wind exerts the highest traction with the most constant direction where the air current can move along unhindered in a tangential direction (White, Mot- tershead, and Harrison, 1992; Häckel; 1993). This is the case on the two lateral trunk faces adjacent to the frontally wind-exposed face. At a microscale, there is additional wind shelter due to “valleys” of the bark relief or to neighboring thalli (Kershaw and Larson, 1974; Nicolai, 1985). Thus, the thalli that were situated on such lateral trunk faces without being wind shielded on a smaller scale could each be divided into an exposed and a sheltered thallus face: wind-exposed branches grew in the direction of main wind exposure, and sheltered branches grew away from that direction; intermediate areas were not considered (see example in Fig. 3).

Solar radiation is independent of the height on the trunk, except in the parts shaded by the crown and at the very base of the trunk, which is more perpendicularly inclined to solar radiation (Stoutjesdijk, 1992). On the other hand, there is a decrease of solar radiation from the south and southwest-exposed trunk faces towards east and west faces and eventually towards the north faces (Geiger, 1961; Nicolai, 1985). The bark’s microrelief does not have a strong effect on incoming solar radiation because of the sun’s changing position throughout the day and the year (Nicolai, 1985).

Supply of rain and snow is at its highest below those points where the crown drains precipitation onto the trunk (stem flow). The drainage zones are ~10–60 cm wide, range from the crown to the trunk base, and can be easily recognized from the strong cover of algae or even mosses on the bark (Matthey et al., 1989).

Morphogenetic patterns of E. prunastri—Branches—The tip of a branch develops one branch pattern per year. Branches mostly grew along their young parts within the last two branch points, which was observed 155 times compared to only 46 cases of increase in older parts of branches (distributed over 15 sufficiently focused thalli on five large-scale photographs from year 1). Some parts of branches were uniform, flat, even, and branched isotomic-dichotomously, whereas others showed numerous irregularities in cross section, growth plane, and branching pattern (Fig. 1).

Complete thalli—Growth forms of complete thalli could be characterized as a combination of different “architectural elements.” These architectures determined whether the thalli became crown-, shrub-, roof-, cave-like, bristly, layered, etc. A branch’s growth plane was either parallel or perpendicular to the trunk (standing off the trunk). Thalli with much growth of branches parallel to the trunk were flat; those with a greater proportion of perpendicular branches were more spherical. Changes of growth planes (see Fig. 1) shaped the growth form in the different sections of a thallus (Fig. 2). Predominant changes from parallel to trunk to perpendicular to trunk resulted in a loose-mesh growth form of the thallus. Predominant changes from perpendicular to trunk to parallel to trunk resulted in a dense, encapsulated growth form.

Comparisons and statistical treatment—The type of cross section of the single branches was assessed on the large-scale photographs and
Cross section | Branching pattern | Growth plane inclination/orientation
---|---|---
Regular growth | Flat, even, rounded at the edges | Isotomic-dichotomous | Even/constant or deviating up to max. 40°
A | Tips of branches rounded and brownish
Irregular growth | Corners along edges, phycobiont layer often and cortex sometimes absent, cortex often with furrows | Isotomic-dichotomous | Tilted/deviated
B | Tips of branches are short stumps, sometimes without cortex, not brownish, mostly with furrows | Anisotomic / polytomous, in extreme cases mutilated | Even/constant
C

Fig. 1. Typical morphological features of *E. prunastri* branches. For quantitative analysis see Table 1.
A consistent analysis of (a) and (b) was preferred. Corresponding thalli from the two heights. In (b) a chi-squared goodness-of-fit test was used to eliminate interthallus variability (described in Fig. 2). Pairwise comparisons (Wilcoxon test) were considered in one comparison due to the lower magnification. In that case the respective three successive observations from August to April were averaged to avoid pseudoreplication.

The growth type was also compared between branches with and without preceding artificial injury (chi-squared test, suitable for frequency distributions).

The amount of grazing (expressed in percentages, i.e., not as a frequency) was compared between inner and outer parts of the 43 thalli from an oak (site 5, see above). The two values for each separate thallus were considered pairwise, in order to eliminate interarea variability. (2) A repeated-measures ANOVA was performed on the single measurements averaged to avoid pseudoreplication. This eliminated the interarea variability. (2) A repeated-measures ANOVA was performed on the single measurements at each date [after ln(x + 1) transformation of the data to nearly normal distribution]. This test considers the dependence between the values collected repeatedly from one trunk area. Chi-squared or Fisher tests were used whenever the growth speed and especially the growth density of directly neighboring single branches might not be mutually independent.

Statistics were calculated with a SYSTAT 5.0 computer package (Wilkinson, 1992). All Wilcoxon tests, Mann-Whitney U tests and ANOVAs were two tailed.

### RESULTS

**Correlation between cross sections and growth types of branches**—Asymmetries in cross sections almost always preceded variations of growth planes or branching patterns in time (i.e., on sequential photos), and occurred behind them (i.e., towards the older, basal parts of the thallus on the same photo), and thus probably induced them (Table 1, Fig. 3).

**Correlation between arthropod grazing and the growth of branches**—Structure—Several common grazers on *E. prunastri* left behind shallow hollows as feeding traces in the cortex and phycobiont layer (*Cerobasis gastijalica* [Psocoptera, Insecta]; *Orchesella cineta* [Collembola, Insecta] and adult specimens of *Carabodes labyrinthicus* and *Phauloppia lucorum* [Oribatei]). Feeding traces of adult oribatids differed from those of other species in having furrows at the hollow’s bottom (Fig. 4a). Freshly regenerated feeding traces in the cortex and phycobiont layer were often recognizable as depressions in the branch’s surface that were covered by a smooth, intact, and clean cortex, frequently showing a furrow relief. Below this cortex the phycobiont layer was sometimes not rebuilt (Fig. 4b).

<table>
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<tr>
<th>Branch with cross section like</th>
<th>. . . developed branching pattern like</th>
<th>. . . developed growth plane like</th>
<th>. . . occurred in front of a younger part of the branch with growth plane like</th>
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<tr>
<td>. . .</td>
<td>A</td>
<td>A</td>
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</tr>
<tr>
<td>A</td>
<td>7</td>
<td>0</td>
<td>48</td>
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<tr>
<td>C</td>
<td>0</td>
<td>9</td>
<td>5</td>
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Fig. 2. Different growth forms of two thalli that grew at wind-sheltered (I) and strongly wind-exposed sites (II) (schematic drawings). For clarity only one out of five to seven branches is drawn. Letters indicate “architectural elements,” which include a change of the inclination of the growth plane. A = growth plane of branch changed from trunk parallel to perpendicular to the trunk, B = growth plane changed in opposite direction than A. The subscripts k, c, p or pm refer to the position within the thallus: base, center, periphery near the tip, or periphery near the margin of the thallus, i.e., closer to the trunk. Greenish-grayish upper sides of branches are hatched, arrow indicates positions of corner along edge of branch (see Fig. 4 for larger magnification). Scale bar = 1 cm.
Distribution—Branches that were sheltered by outer branches were grazed on 2.1 times more of their surface area than the unsheltered ones at the periphery of the thallus (\(N = 43\) thalli, \(P < 0.001\), Wilcoxon rank test). Along the wind-exposed faces of the 43 thalli the branches were almost ungrazed (for determination of wind exposure see Materials and Methods section). Along these most exposed faces the proportion of branches with cross sections showing irregular growth (Fig. 1) was significantly smaller than along the more sheltered thallus faces [\(\chi^2 = 4.03, P < 0.05\), \(N = 91\) branches on three trunk areas (= five thalli) in year 2; Fig. 3].

Thalli from 1.7 m height above ground level did not differ significantly from thalli at 0.5 m height in the proportion of surface area grazed (factor 1.25, \(N = 43\) thalli, \(P = 0.27\) according to Mann-Whitney \(U\) test), nor was the number of changes of growth planes from trunk parallel to perpendicular or vice versa significantly different at the two heights (factor 1.13, \(P = 0.77\), Mann-Whitney \(U\) test, \(N = 43\) thalli). Growth plane changes were recorded as presence of parallel/perpendicular, and perpendicular/parallel changes in the four sections of each thallus (presented in Fig. 2); differentiation of single branches, growth points, or cross sections was impractical.

Thalli of \(E.\) prunastri var. herinii were recognizably more grazed upon than the neighboring specimens of \(E.\) p. \(p.\) prunastri with the latter’s higher lichen acid contents (\(N = 20\) thalli were found). Also the number of branches with corners along edges or with destroyed tips was much higher in any \(E.\) p. var. \(h.\) herinii. The growth forms of \(E.\) p. var. \(h.\) herinii were denser and more hemispherical than that of any neighboring \(E.\) p. var. \(p.\) prunastri of the same tree (Fig. 6a).

On thalli with abundant epiphytic algae animal feeding traces in the cortex and phycobiont layers were extremely sparse; the animals grazed in preference upon the epiphytic algae that were not protected by a cortex layer and were therefore much more easily accessible (Prinzing and Wirtz, 1997). These thalli were much more regular in growth than neighboring “normal” specimens (based on 65 algae-covered thalli at all three sites where both types were growing next to each other [Fig. 6b]).

Correlation between climatic exposure and the growth of \(E.\) prunastri—Increase and shape of differently exposed branches—An increase in size at the tips of branches that were exposed to wind (for determination of exposure, see Material and Methods section) was observed only 49 times in comparison with 106 times under windsHELTERED conditions (2–3 mo periods from August to April of year 1, with 15 sufficiently focused thalli distributed over five photographed trunk areas; Fig. 7). A greater increase in branch size in sheltered than in exposed parts of branches was also found when considering the relative numbers of observations of branch size increase (number defined as [number of observations of size increase within 2–3 mo]:[total number of visible branches]; results: repeated-measures ANOVA: \(P = 0.05\), Wilcoxon test: \(P = 0.043\), \(N = 43\) thalli). Moreover, branches were more densely packed at wind-exposed thallus faces (branch density = [the number of branches that were close to their neighboring branches, i.e., separated by less than about twice the branch’s thick-
Fig. 4. Branch with feeding traces (a, January) and the subsequent regeneration and changes in growth plane (b, the following April). Right end of branch in cross section indicating C = cortex, P = phycobiont layer, M = medulla layer. (a) In feeding traces (indicated 1–5) cortex and phycobiont layers were eroded and the medulla was exposed. The same was found at a rupture zone (6). The bottom of many feeding traces had a furrow structure (4 and left part of 2). Outline and cross section (right) appeared symmetrical, the growth plane was even and constant. (b) Many feeding traces were covered by a cortex already (2–4), but in some cases no phycobiont layer was regenerated (3 and 4, at the latter the light underside now reached far up on the edge). Even after regeneration shallow hollows and furrows persisted in the branch’s relief. In the cross section a corner along the edge did persist (S). The growth plane corresponded to the new asymmetry of the cross section and inclined (large gray arrows). Scale bar = 0.5 mm.

Fig. 5. Two examples of development of branches with natural (filled triangle) or artificially induced (filled square) corners along edges, or with intact, rounded edges (unfilled circle) between January and April. The orientation and inclination of branches are indicated by their darkness (frontal positions are lighter). Growth planes of branches almost always inclined along the natural or induced corners. Undamaged growth points were almost always unchanged. Scale bar = 2 mm.

ness] ÷ [overall number of visible branches]; results: repeated-measures ANOVA: $P < 0.001$, Wilcoxon test: $P < 0.02$, $N = 7$ photographed trunk areas with 18 thalli sufficiently focused). As mentioned above, the frequency of branches with irregular cross section (Fig. 1) was proportionally smaller on the exposed than on the more sheltered thallus faces.

**Growth forms of complete thalli under different exposure**—The correlation between wind exposure and growth form corresponded to the attractiveness of the thalli to grazers (corresponding to few epiphytic algae as alternative food for grazers vs. much cover, and to a lesser degree also to very low lichen acid concentrations in *E. p. var. herinii* vs. *E. p. var. prunastri*). In strongly grazed thalli the growth form corresponded to differences in each of the following classes of wind exposure (see Materials and Methods): within the microrelief, between different faces of a trunk, and at different trunk heights. More exposed thalli appeared to be denser and more aerodynamic (recognized on each of the 56 trees at 24 sites in >70% of the thalli lacking an abundant cover of epiphytic algae: examples in Fig. 7).

In thalli with little grazing (conditions opposite to the above mentioned) such a differentiation of growth forms was not observed (Fig. 6). In a few cases the branches were found to be bent slightly but consistently in the same direction. Sometimes the wind-exposed parts of the less grazed thalli were smaller (e.g., in the upper zone of the *E. p. var. prunastri* thallus in Fig. 6a).

Sunlight is distributed differently on the trunk surface than wind (see Materials and Methods). Thus sunlight exposure did not match any of the above-mentioned patterns of thallus growth, nor any other recognizable growth pattern, nor were any of the above-mentioned patterns in growth form correlated with crown-drainage zones on the trunk where precipitation is most intense. Sometimes a luxuriant, hanging growth of thalli was striking there.
Mechanical effects of wind—Falling off the bark was the most common cause of death observed for *E. prunastri* in the area of investigation (Fig. 7: X). This happened mainly during strong wind with simultaneous precipitation. And, in fact, detached parts of thalli (i.e., photographed parts of thalli that were later found missing on subsequent photos) were demonstrated to have had a more wind-susceptible (i.e., loose and unaerodynamic) growth form compared to undetached neighboring parts of thalli (confirmed in 47 out of 52 observations in year 1 in all small- and large-scale photographs of 11 trunk areas with missing thalli: example in Fig. 7). Also, the corresponding single branches that became detached by wind were more regular (see Fig. 1) than neighboring, intact ones (65 out of 91 observations of single branches). All of the 88 collected thalli that had been torn off the trunk were rather regular in growth pattern. The algae cover of these thalli (as a possible indicator of the attractiveness of the lichen phycobionts for grazers) was not assessed because it might well have been affected by the microclimate, grazers, and fungi at the ground where the thalli had been collected. Detachment of thalli by vertebrates was rarely observed: squirrels were very rare, and birds collected thalli only exceptionally and only during spring (as nesting material).

Wind also bent branches when they were soaked, flexible, and mostly spread away from the trunk. When such branches dried out under windy conditions, they became stiff and temporarily fixed in their flexed position.

**DISCUSSION**

An important prerequisite for the immense polymorphism of *E. prunastri's* complete thalli is a variation in
Fig. 7. Growth and rupture of branches of *Evernia* at differently exposed microsites, August (left) until January (right). Line drawings illustrate features on photos. On a small scale there was a high diversity of growth forms. Those in January matched the wind exposure in the microrelief well; on the left (i.e., most wind exposed) faces of thallus branches were directed lee-, down-, or trunkwardly, resulting in a more streamlined shape of the thallus surface. Two examples are ringed, the lower one being much more drastic than the upper one. Increase at tips of branches from January to August was smaller in wind-exposed than in wind-sheltered zones. Examples are indicated by numbers and presented as magnified line drawing below the photographs. Detachment (from August to January, indicated by X) occurred for branches that grew on wind-exposed faces in a very loose or wind-opposed manner (in August). Scale bar = 5 mm.

growth of their single branches. The causes of this variability shall be discussed first. Afterwards, processes that controlled the growth form development shall be explained. These small- and large-scale processes are included in a graphical model (Fig. 8) that helps to identify equivalence with processes in other cryptogams.

Single branches—Observation of single branches revealed a close correlation between their cross sections, their growth planes, and branching patterns. A strong deviation from the horizontal inclination and orientation was related to corners along edges of branches; an anisotomic-polytomous branching pattern was related to cor-
Table 2. Correlation of wind exposure, grazing, and their combination with the predominant growth of branches and with the complete thallus growth forms of 

<table>
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<tr>
<th>Grazing intensity</th>
<th>Wind-sheltered positions</th>
<th>Wind-exposed positions</th>
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<tr>
<td>VERY LOW</td>
<td></td>
<td></td>
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<tr>
<td>On outer branches of wind-exposed thallus face</td>
<td>—</td>
<td>Branches: mostly regular (Figs. 1, 3)</td>
</tr>
<tr>
<td>On thalli with dense algae cover</td>
<td>Branches: regular (see Figs. 1, 6b)</td>
<td>Complete thalli: regular and loose (Fig. 6b, algae-covered thallus)</td>
</tr>
<tr>
<td>NORMAL (E. prunastri without or sparse algal cover)</td>
<td>Complete thalli: rather loose, mainly the wind-sheltered face (Fig. 2-I)</td>
<td>Complete thalli: dense layers, mainly on the wind-exposed face (Fig. 2-II)</td>
</tr>
<tr>
<td>VERY HIGH</td>
<td></td>
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<tr>
<td>On E. p. var. herinii</td>
<td>Complete thalli: very irregular, mainly loose and bristly (even more loosely than Fig. 2-I)</td>
<td>Complete thalli: very dense and bushy, almost closed at the outside (even denser than Fig. 2-II)</td>
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Fig. 8. Interaction of processes determining the growth form of 

_Evernia prunastri_ thalli. Numbers are referred to in the Discussion. Wind-acclimated growth forms of whole thalli develop ontogenetically due to a faster growth in those parts of branches directed into wind shelter at the respective microsite. The necessary trigger for variation in growth directions is largely generated by grazing.

ner- or crater-like injuries at their tips (Fig. 8: 4). Such corners along edges or tips of branches were themselves induced by injuries. This strengthens the impression of Stone and McCune (1990) that anisotomic-polytomous branching patterns of branches are caused by injuries at the branch tips.

Grazing, natural or simulated, apparently caused most of these injuries and irregularities of branch growth (Fig. 8: 3) in my study. Further causes might have been wind or any windborne particles, e.g., sand or ice crystals (Häckel, 1993). But grazing seemed to be the prevailing impact, because of (a) the coincidence in the distributions of irregular growth and of grazing but not of wind (Table 2: comments on branches), and (b) the structural similarity between feeding traces and corners along edges/destroyed tips of branches.

Where the growth of branches was not disturbed by grazing they mainly developed symmetrical cross sections, rounded edges, and had a constant growth plane and isotomic-dichotomous branching (Fig. 8: 1, Table 3). In the model in Fig. 8 variable branch growth (point 5) is thus presented as a direct consequence of symmetric patterns (cross sections) altered by exposure to external disturbance.

In basal branches, which were hidden from photographic observation in the present study, a third type of asymmetries in branch cross sections was sometimes observed: strong infoldings of the lower side of branches into the medulla correlated to extreme bending. Such asymmetries were often found to be correlated with mining by juvenile oribatids (Prinzing and Wirtz, 1997). These animals then enlarged their tubes into the medulla, increased the risk of a rupture toward the branch’s upper side, and enhanced the morphogenetic effect of cross sections with such infoldings on further branch growth. Similar cases of mining by oribatids in the medulla of lichen thalli including ruptures to the branch’s upper side are described by Travé (1963) and for fruticose thalli similar to _E. prunastri_ by Bachmann (1929) and Bellido (1979). Bachmann also shows how such tubes lead to strong infoldings and deep groves in branch cross sections. Zopf (1907) found that branches of fruticose lichens also become hollow and wider when mined. It is therefore probable that in _E. prunastri_ also the juvenile oribatids could not only have enhanced the effect of tube formation and infoldings in branches, but even induced them. I did not observe any other organisms that create/enlarge such tubes in _E. prunastri_, nor did I observe tubes that were too narrow or too wide to be attributable to the effect of a juvenile oribatid.

**Complete thalli**—The growth form of complete thalli, especially the branch density, matched the wind exposure only when the branches were also grazed upon (Table 2). Without grazing wind exposure did not have a clear effect on growth form besides occasional bending of branches. Without wind exposure (on wind-sheltered faces of thalli or trunks or in bark valleys) all growth forms were rather loose and susceptible to air currents.

The described variation in growth form even on differently exposed faces within the same thallus would have hardly been conceivable if all the single branches had been growing evenly and isotomic-dichotomously. Instead, such differentiated growth forms were able to develop, if (a) branches, including the young ones, were...
variable in their growth (Fig. 8: 5) and if (b) among such branches those increased fastest that grew into a wind-sheltered direction (Fig. 8: 6). Both of these conditions can be demonstrated. From Fig. 8 the mechanism can now be recognized that is probably most relevant for the observed interaction between grazing and the ontogenetic ability to vary complete growth forms; grazing disturbance mainly generated the variability of the branch growth, i.e., one of the prerequisites for growth form differentiation.

The observed selective effect of wind on growth speed could have been caused by (a) convective desiccation of the psikolohydric thalli, (b) minute cracks in the cortex or its superficial erosion as a result of microscopic abrasion, (c) ruptures of the cortex when branches are bent by wind, or (d) the stress effects of shaking. All such mechanisms have already been demonstrated for phanerogams (Nobel, 1981). Convective cooling by wind might have additionally reduced metabolism while thalli were still wet, whereas it could not have led to serious chill damage since this occurs in lichens only at extremely low temperatures (Henssen and Jahns, 1974).

Ultimately, these processes of induced variation and selective growth lead to thallus growth forms that are phenotypically acclimated to wind (Fig. 8: 7). These ontogenetic, modifying processes mimic to some degree processes in the phylogenetic evolution of adaptations (Darwin, 1859). The ontogenetically acclimated thalli were much less endangered by wind dislodgment than those of non-wind-acclimated growth forms showing growth patterns that are very regular and simple (Fig. 8: 2). The aerodynamic effect of such wind-acclimated, dense growth forms is demonstrated by a desiccation experiment (Prinzing and Wirtz, 1997): wet thalli are dried with a hair drier from a fixed position and distance in front of the thallus for 1 min. The percentage of water loss of different thalli indicates the wind accessibility and turbulence at the surface of the respective thalli. This water loss correlates well to a decreasing branch density of the frontal faces of thalli ($r = -0.96, P < 0.001$).

The basic adaptive value of shrubby growth forms is apparently the same as in crowns of phanerogams (Nobel, 1981): an aerodynamic shape with a mutual sheltering of branches. Morphogenetic processes analogous to those in Fig. 8 (simple growth patterns, environmental disturbances e.g., grazing and selective influences on growth speed) are found in the phanerogam root system and they result in an analogous polymorphism with advantages to different forms in different contexts (Simberloff, Brown, and Lowrie, 1978; F. Hallé, URA, Montpellier, personal communication).

How do other species of fruticose cryptogams exposed to turbulent currents develop stable thalli? In many taxa, thalli can generate high variability in branch growth on their own, without additional disturbance by grazers. This could be due to rounded cross sections of branches (e.g., the lichen genera Usnea, Cladonia, Stereocaulon, mosses, and some calcareous red algae). Such cross sections do not lead to a branching symmetry, i.e., there is no pattern analogous to 1 in Fig. 8 and thus processes 3 and 4 (Fig. 8) are superfluous. Fruticose cryptogam species with more flattened branches often have apical, spirally dividing cells (Phaeophyceae) or actually consist of bunches of cell threads each dividing dichotomously but oriented into separate directions (multiaxial Rhodophyma). Here, the variable growth of branches (analogous to 5 in Fig. 8) depends on asymmetries on a cellular level, instead of asymmetries in the branch's cross section (4 in Fig. 8).

In many species of benthic fruticose algae branches grow symmetrically and nonvariably. Thallus growth forms are correspondingly even, often fan-like, and very susceptible to water current (analogous to 2 in Fig. 8). And in fact these thalli do not have rigid growth forms that remain unmodified by water movement, but instead their soft, water-saturated bodies can flexibly "match" these currents. The risk of detachment is reduced by a cartilaginous or leather-like consistency. Moreover, populations of many marine benthic fruticose algae can easily compensate for occasional detachment because they are able to grow much faster than terrestrial epiphytic lichens.

In all these examples grazing is not necessary for a morphogenesis of current-tolerant thalli. But there are still many fruticose, terrestrial cryptogams with flat branches, lacking spiral growth patterns. It would be very interesting to find out their strategies to cope with wind exposure and to test the importance of grazing. The existing qualitative descriptions of grazer-induced variation in such fruticose lichens (Zopf, 1907; Bachmann, 1929) suggest that the mechanisms might be similar to those in E. prunastri.

Compared with the indirect beneficial effects of grazing, the detrimental direct effect might be of subordinate importance for those thalli that grow on strongly wind-exposed positions. It is at exactly such exposed trunks and positions within the bark relief that the grazers do prefer E. prunastri most (compared to other lichens; Prinzing, 1996, 1997). A completely detrimental effect of grazing has until now only been found under wind shelter on trunks in a forest (extreme overgrazing reported by Laundon [1971]). Mostly, however, the thalli are protected because grazing is always restricted to certain specific regions within a thallus shrub depending on the surrounding climate (Prinzing and Wirtz, 1997).

**Literature Cited**


