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PLANT PUBESCENCE: AN ECOLOGICAL PERSPECTIVE

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GENERAL DISTRIBUTION

The epidermis of plant organs is often ornamented with outgrowths called trichomes or hairs (Esau, 1965). Essentially all the major groups of terrestrial plants appear to have or have had the capacity to develop such structures. The statement by Uphof (1962, pp. 194–195) that trichomes are not to be found on certain major taxa such as the Lycopodiales, Ginkoes, Coniferae and Chlamydospermae, is an obvious error since hairs have been observed in all four of these groups. The fossil *Sigillaria*, a close relative of the present-day Lycopodiales, has hairs on its leaves (Delevoryas, 1962). Variation in the hairs on the twigs of *Picea*, one of the Coniferae, are used in the characterization and identification of different *Picea* species (Fernald, 1950). I have personally observed trichome-like structures on the young shoots of *Ginko biloba* L., the only living member of the Ginkoales, and

Gnetum montanum Markgraf., a representative of the so-called Chlamydospermae. Even Bryophytes commonly show hairlike outgrowths, e.g., *Aulocomium palustre* (W & M) Schw., *Dicranum fulum* Hook., and *Mnium punctatum* Hedw.

The peak of trichome development is found in the ubiquitous flowering plants, however, and any consideration of the ecological significance of such structures must deal mostly with the members of this group. Carlquist (1962) observed that very few species of Angiosperms are truly glabrous and suggests that those that are must have been derived from pubescent ancestry. Netolitsky (1932) proposes that every epidermal cell has the potential of forming a trichome. Even so, trichome production is more conspicuous in some taxonomic groups than in others. Such differences are apparent at the class level of Monocotyldeonae and Dicotyldeonae. Even though the range of trichome types found in monocots (Stauderman, 1924; Hummel and staesche, 1962) is about equal to that found in doctos (Metcalfe and Chalk, 1950; Hummel and staesches, 1962), the frequency of distribution of the different morphological types among the species of the monocots is more restricted and does not show as much diversity. Also, when the trichomes are present, the tendency for them to form a dense indumentum is apparently more pronounced in the dictos.

Arthur Cronquist has suggested to me that the almost universal tendency toward trichome production among higher plants may be related to the necessity for root hairs. It can be argued that essentially the same genetic system should be required for both root hairs and trichomes. The necessity for the assimilatory function of root hairs is clear cut. On the other hand, questions about the evolutionary significance of trichomes have been the subject of much speculation, over the years. It should be noted in this regard that, because the propensity for trichome production is so ubiquitous in the plant world, the potential for the development of a hairy covering must be available in the gene pool of plants occupying essentially all terrestrial environments. Thus if selection pressures have been important in directing the development of pubescence, there should be patterns of correspondence between its occurrence and the presence of particular environmental conditions.

TRICHOMES AND THE INDUMENTUM

Epidermal appendages may be viewed from two different perspectives: (1) the nature of the individual trichomes themselves, and (2) the characteristics which collectively they impart to the surfaces upon which they are borne, i.e. the nature of the indumentum layer as a whole unit. In this regard Robert Hooke (1665), noting the nature and variety of plant hairs, was impressed to speak of them as "secondary plants" while his contemporary, Nehemiah Grew (1672) seemed equally impressed with the indumentum as a whole and spoke of the "hairy skins" of plants.

In the literature a distinction between the kinds of trichomes and the structure of the indumentum is not often clearly drawn. Terms used in plant descriptions pertaining to the indumentum (e.g., tomentose) are frequently used in ways which seem to be parallel to those pertaining to the structure of individual trichomes (e.g., stellate). A distinction between the kinds of trichomes as opposed to the kinds of indumenta is important in an ecological context since it is likely that the environment has a greater influence in modifying the indumentum than in changing the type of trichome. Selective pressures resulting in indumentum convergence can easily cut across phylogenetic lines, since the indumentum is not so much influenced by the morphology of the individual trichomes as by their distribution and density; a plant with stellate hairs may have a very thick, velvety indumentum or a sparse one, depending on the number of hairs per unit area. So also, a plant with simple linear hairs. Thus, trichomes of rather different morphology may be assembled in ways that when viewed as collective units appear very similar. Nevertheless, trichomes are the basic building blocks from which indumenta are made and merit consideration in some detail before a discussion of the different ways they may be arranged on plant surfaces to form different kinds of indumenta.

The Nature of Trichomes

Trichomes originate from epidermal tissue and then proceed to develop through growth, differentiation or cell division so as to produce hair-like projections extending from the epidermal surfaces. They can be seen with the unaided eye on many plants, but most are just small enough so that only their bare outline can be discerned. In the early days of the microscope these barely-visible structures became popular subject material for study and through the years a great volume of literature about their structure, development and probable functions has accumulated. Reviews of the literature have appeared periodically (Weiss, 1867; Netolitsky, 1932; Uphof, 1962). Much of the work specifically pertaining to plant hairs was done in the past century or the early part of this one. Little new information on their general morphology and anatomy has come to light in recent years. The fine structure, however, is being actively studied by many investigators at the present time. Morphologically, trichomes exhibit a broad spectrum of variations, ranging from flat plates to elongate highly ramified outgrowths; some are unicellular and others multicellular; some have enlarged tips and others enlarged bases. Some remain metabolically active throughout the life of the organ upon which they develop, while others function metabolically for only a short period and then die, after which they may either persist or be shed.

Developmental patterns are not easily categorized since hairs are produced on almost all plant organs at various stages of development. Hairs may mature early relative to other organ tissue, as on the stems of *Melampyrum nemorosum* L., where full development takes place in a few days (Miroslavov, 1958); or they may continue to develop over an extended period as does the ovular cotton fiber, which takes 20-30 days to elongate and then about the same amount of additional time to reach final maturity (Tharp, 1965).

The initiation of new development may be related to environmental factors as well as genetic endowment. For example, Mohr (1959) reported that the initiation and growth of trichomes on the hypocotyl of *Sinapis alba* L. were responsive to light quality. Hair production was stimulated by red and inhibited by far-red radiation, a typical example of the phytochrome reaction. Blue light at high intensities produced results similar to those of red light.

As trichome differentiation proceeds, specialized types of cells and cell structures become evident. The cellulosic microfibril matrix of the cell walls may remain almost pure cellulose or become impregnated and incrusted with lignin, carbonates and silicates (Uphof, 1962; Kaufman et al., 1972). The cell walls may remain relatively thin or become so thickened that they almost occlude the cell lumen. The degree of thickening may vary from cell to cell in multicellular hairs, or from one site to another within individual cells of both multicellular and unicellular types. A reduction in thickness is frequently observed at the site of breakage (disarticulation zone) when trichomes are shed. Wall pitting is common, especially on the inner surfaces of cells in contact (Inamden et al., 1973; Johnson, 1968). Outer cell wall surfaces often exhibit various forms of ornamentation in the form of ripples, bumps, and projections resulting from changes in microfibril orientation during growth, as well as the deposition and accumulation of carbonates, silicates, etc. (Metcalf and Chalk, 1950; Haberlandt, 1914; Uphof, 1962; Esau, 1965; Kaufman et al., 1972). The cuticle of the epidermis is continuous over the trichomes although it is not necessarily of uniform thickness throughout (Esau, 1965; Uphof, 1962).

The contents of trichome cells are similar to other epidermal cells at first, but as differentiation proceeds shifts in the organelle and cytoplasmic complement may take place. A strong development of mitochondria and a complex membrane and wall structure have been noted in trichomes of *Tillandsia usneoides* L. (Dolzmann, 1964, 1965). An increase in dictyosomes, both in size and number, along with a compacted endoplasmic reticulum bearing a high number of ribosomes have been reported for the glandular hairs of *Mentha piperita* L. (Amelunxen, 1964). Schnepf (1968) and Heinrich (1973) have found a similar elaboration of dictyosomes in trichomes of *Rumex, Rheum,* and *Monarda.* Cell nuclei are often enlarged by endomitosis. Tschermak-Woess and Hasitschka (1953) reported endopolyploidy in the trichomes of 18 species with the basal cells of *Bryonia dioica* L. reaching a high of 256 N. Endomitosis is apparently common in secretory trichomes (Tschermak-Woess and Hasitschka, 1953; Heinrich, 1973). However, the trichomes of some other 46 species from 32 plant families surveyed by Tschermak-Woess and Hasitschka (1953) failed to show endopolyploidy. Plastids and even chloroplasts are sometimes present (Uphof, 1962). Older cells become highly vacuolate and may contain various kinds of inclusions, e.g. druses, raphids and starch grains (Uphof, 1962). Many trichomes lose all of their contents as they pass through their developmental phase.

Several different trichome classification schemes have been proposed (Guettard, 1745; Schrank, 1794; de Candolle, 1827; Weiss, 1867; Rauter, 1872; Suckow, 1873; de Bary, 1877; Solereder, 1908; Netolitsky, 1932; Hummel and Staesche, 1962). Morphological and functional criteria provide the basis for all schemes and reveal the features considered most significant by the individual authors. The schemes of Schrank, Weiss, Solereder, Netolitzky, and Hummel and Staesche make a primary distinction between glandular and non-glandular types, with further characterizations on the basis of such features as the number of cells and the cell arrangements. De Candolle stressed the site of occurrence on the plant, whereas Guettard and Rauter emphasized developmental considerations such as tissue of origin and mode of attachment. Metcalf and Chalk (1950) in their treatment of the anatomy of the dicotyledons name over 50 different types, but refrained from presenting a classification. A distinction is sometimes drawn between trichomes and emergences (Sachs, 1873; de Bary, 1884). The latter are defined as surface processes with their origin wholly or partly in subepidermal tissue while the former are entirely derived from the epidermis proper.

Many of the categories within the earliest classification schemes were not mutually exclusive and as a result a given trichome could fit more than one description. The recent systems are more definitive and usually provide a reasonable basis for assigning a given trichome to only one category, e.g. Hummel and Staesche (1962). The interest in trichomes over the past few years has been sustained mainly by taxonomists who have found them most useful for purposes of classification (Stace, 1965; Mosquin, 1966; Carlquist, 1961; Cannon, 1909; Schmid, 1972).

The Nature of the Indumentum

The indumentum as here defined is the collective trichome cover of a given plant surface. Pubescence, in the general sense of the word (Benson, 1957), is a synonym and will be used interchangeably.

Patterns of Occurrence. The trichome cover of individual plants commonly varies in quantity (trichome size and density) and quality (trichome type) from organ to organ, and from tissue to tissue (de Candolle, 1841). A dense covering often develops on young organs. As the organs expand through growth, the original trichomes are spaced further and further apart, and if no more new ones are produced, a sparse indumentum will result at maturity. On the other hand, trichome production may keep pace with the expanding surface so that a dense indumentum is always present. When trichome production continues through ontogeny, different kinds of trichomes may be produced at different stages of development, e.g. the floral bracts of *Cannabis sativa* L. give rise successively to 3 morphological types of glandular trichomes (Hammond and Mahlberg, 1973). Different trichome production may also be evident for different parts of the same organ. Thus, an enhanced indumentum development on leaves is commonly observed on the abaxial surface, above vascular strands and along the margins (Johnson, 1968).

In addition to the patterns of hair production noted in relation to the ontogeny of individual organs are others which correspond to the development of the entire plant. Thus Yapp (1912) working with *Spiraea ulmaria* L. and Stober (1917) working with several species of herbs report that upper stem leaves tend to be more pubescent than leaves born toward the base of the plant. Also, the first spring leaves of *Spiraea ulmaria* are glabrous but subsequent ones become more and more hairy until the middle of the summer, at which time the trend is reversed, so by late fall only glabrous leaves are produced again (Yapp, 1912). Similarly three species of *Zauschneria* (*Z. cana* Greene, *Z. californica* Presl, and *Z. septentrionalis* Keck) produce large spring leaves that are much less pubescent than the smaller fascicled ones borne late in the summer (Clausen et al., 1940). Whether such patterns of production result from an internally programmed developmental sequence or from metabolic processes set in motion by seasonal changes in the environment is open to question, especially since variations in the radiation and water regimes have also been shown to be correlated with pubescence.

The variable habitat studies with members of the genus *Potentilla* by Clausen et al. (1940), provide prime examples of the general trends. They found that the clonal material planted in dry, sunny habitats was strikingly more hairy than the same material cultivated in the shade. In the case of *P. pectinisecta* Rydb. and *P. flabelliformis* Lehm. the increase in density was not entirely attributable to differences in leaf size, however, but reflected an actual increase in the numbers of hairs produced per leaf.

Examples of more strict genetic control are also known. Individuals from a population of *Erigeron salsuginosus* (Pursh) Greene growing in a meadow differed in the amount of pubescence shown and when transplanted to a uniform garden retained the differences. In a few other cases the genetic control seems to be so tight as to allow only either-or alternatives. Three species called to my attention by Rupert Barneby of the New York Botanical Garden (*Mirabilis pudica* Barneby, *Amsonia breviflora* Gray, and *Cyclandenia humilis* Benth.) are usually entirely glabrous, but also have densely pubescent forms with no intermediates. The pubescent forms of *Amsonia* and *Cycladenia* have by some authors been accorded species and varietal rank, respectively, being given the epithet *tomentosa* (Munz and Keck, 1959). It is obvious that the principal differences in these "forms" is merely the presence or absence of pubescence.

Environmental Patterns. If pubescence has ecological significance, its pattern of occurrence should indicate how the environment has acted to sort out the genetic material that regulates its production. The evidence from the ontogenetic and developmental observations reviewed above (Clausen et al., 1940) supports the early views of Kerner von Marilaun (1896), Schimper (1903), Warming (1909), Coulter et al. (1911), and Sabnis (1919), that pubescence is positively associated with harsh moisture regimes. This view is exemplified by Warming who contends that in cases where species exist in both xeric and mesic habitats the individuals from the xeric habitat are the most hairy and again by Coulter et al. who state that in cases where species may be either terrestrial or aquatic the terrestrial ones may be hairy while the aquatic ones never are. The other authors report the general tendency for plants of deserts, steppes and alpine tundras to show a high incidence of pubescence.

In recent years numerous taxonomic studies have been published that describe geographic variations in species pubescence. Levin (1973) reviews a number of these and is unable to find a pattern that would support the long-held contention that the drier the habitat, the greater the trichome production. He suggests that gradients of biotic factors as well as physical factors should be considered. The quality of the pubescence then becomes an important consideration, especially in terms of the glandular and non-glandular components. In this regard it should be noted that it is the non-glandular shag-type hairs that usually produce the most dense and conspicuous indumenta and are therefore most likely the types considered by the earlier investigators.

The ecogeographic relationships of pubescence can be best evaluated by looking at whole communities of plant species as opposed to individual taxa. Exceptions to any general patterns that may exist are bound to occur, and the danger of selecting the exceptional taxon is always present. The argument in favor of using the vegetation of whole communities as a basis for general comparisons is of only limited value at this point, since little quantitative information of this sort has been published. Still there are enough data now available to make a start in this direction. McCleery (1906) examined all the species in the state herbarium of Ohio and graded them according to whether the leaves and twigs were (1) pubescent, (2) glabrous, (3) glaucous, (4) granular, (5) scruffy, or (6) resin dotted with punctate or peltate scales. She further subdivided pubescence into glandular, stellate and tomentose types. On the basis of calculations made from her numerical summaries, it appears that 55% of the species in Ohio (a deciduous forest area) are pubescent; of this group 4% are tomentose, 2% stellate and 3% glandular. McMillan (1964) studied the pubescence of four important prairie grasses, and found them to show ecotypic variation with respect to pubescence. All four species (*Andropogon scoparius* Michx., *A. gerardii* Vitman, *Panicum virgatum* L. and *Sorghastrum nutans* (L.) Nash showed their greatest trichome development in the warmer, moister south-eastern part of the North American prairie.

In studies of my own on 4 communities (a sandy beach, an old field, an oak forest and a red maple swamp) representing an increasing moisture gradient in the deciduous forest area of eastern North America, I found the incidence of leaf pubescence to be similar for each community, embracing 70 to 80% of the species present. The quality of the pubescence, however, showed differences from one community to another, becoming more dense with respect to the mature foliage in the drier environments (Johnson, 1968). When the pubescence of immature foliage is considered, a different pattern of production and distribution becomes evident. From this perspective it was found that the mesic oak forest showed the highest pubescence production rate during a period of minimal moisture stress in early spring. Similar patterns are also evident in data from an unpublished study of six North American communities (one forest, three grasslands, and two deserts), where I found little difference in the percentage of species with pubescence among the communities, but that the desert species with pubescence had a much denser covering. It thus seems clear that ecogeographic relationships of pubescence must involve environmental factors in addition to moisture.

Classification of Pubescence. Most regional and local floras as well as elementary texts for taxonomy contain glossaries defining terms used to describe different kinds of indumenta. Four such sources (Fernald, 1950; Lawrence, 1951; Benson, 1952; and Gleason and Cronquist, 1963) were consulted and studied in detail, and the definitions for terms common to the four sources were compared. The following is a summary of the findings from this study that has been reported elsewhere (Johnson, 1968). It was found that in general the indumentum types defined are differentiated qualitatively on the basis of trichome texture, orientation, density, size, color, distribution pattern, and in some cases trichome type. The individual definitions as they are given are not equally based with a systematic consideration of all criteria, but usually depend on only one or two of the possible combinations. Thus, texture is the major emphasis for definitions of downy, pilose, pannose, hirsute and hispid. Texture and trichome orientation play a major role in the definitions of strigose, silky, sericeous and velutinous. Trichome orientation and density appear of primary importance in the definitions of arachnoid, villose, woolly, tomentose, lanate and lanuginous, while trichome distribution patterns provide the primary distinguishing characteristics for ciliate and floccose. The terms canescent and hoary are based on color, while papillose and glandular pubescent depend on the presence of particular types of trichomes.

All the definitions are subjective. In some cases there is almost complete overlap in the verbal description of the terms, cf. silky, sericeous, and villose as well as woolly, tomentose, lanate and lanuginous. Whether such close similarities occur because the definitions actually do pertain to the same thing, or are just inadequate definitions of different kinds of indumenta which the various authors can and do visually distinguish in practice, is debatable. Some drawings corresponding to definitions in the texts by Benson and Lawrence prove helpful in grasping the concepts held by the two authors, but here some apparent difference becomes even more obvious (e.g. their representations of velutinous). It seems desirable that indumentum descriptions be put on a more objective basis. The desirability of establishing distinct categories is questionable, however, since there is an almost continuous gradation among the types that might be recognized. Any quantitative limits put forward to divide this spectrum of variation are bound to be arbitrary. Still it is important to establish some kind of formal criteria by which consistent evaluations can be made if comparative aspects of pubescence are to be studied seriously (Johnson, 1968).

FUNCTIONS ASCRIBED TO PUBESCENCE

The many functions which have been ascribed to pubescence may be conveniently divided into three categories that reflect in a general way the kinds of selective forces which have been implicated in the evolution of indumenta. They are: (1) the adaptations said to be related to factors of the physical environment; (2) those related to the biotic environment; and (3) those related to internal physiological controls.

Relationships to Physical Factors

The presumed adaptive role of pubescence accorded the most emphasis in the literature concerns plant water economies. Plant hairs have been repeatedly linked either directly or indirectly to increased water use efficiency, and at present statements to this effect are commonplace in general textbooks (Fritsch and Salisbury, 1965). The inference that this is so, is readily accepted as an explanation of the evolutionary force which brought about the purported correspondence between pubescence and arid environments. Experimental evidence on this matter is not clear, however, and a rather full discussion is in order.

Boundary Layer Effects on Transpiration. Pubescence should be expected to affect transpiration directly through its influence on the water diffusion boundary layer of the transpiring surface of a leaf. A layer of hairs will in most cases decrease the air movement next to the leaf, and thus create a greater thickness of still air through which water vapor must diffuse in moving from the saturated leaf interior to the drier air outside (Woolley, 1964). This relationship is a special case of what has been termed boundary layer resistance. The basic physical phenomena involved in determining boundary layer resistances are well understood (Gates, 1968), but the magnitude of this resistance relative to other diffusive resistance, particularly those associated with stomata, is confused in the literature. The relationship between the stomatal and boundry layer resistances is of great significance in attempting to assign an adaptive role to the indumentum layer in this connection. Two kinds of experiments performed by a variety of investigators have a bearing on the matter.

The first group of experiments concerns the transpiration rates of pubescent vs. non-pubescent species, and the second the transpiration rates of pubescent individuals or leaves of individuals in natural and shaved condition. In the first instance Sayre (1920) compared the transpiration of densely pubescent *Verbascum thapsus* L. with less hairy tobacco plants and found that *Verbascum* had the higher rate. Cooper (1922) found that *Arctostaphylos tomentosa* (Pursh) Lindl., having a dense indumentum, had the highest transpiration rate among three species of chaparral plants tested. Shapiro and DeForest (1932) likewise found the densely pubescent *Salvia apiana* Jepson to use water at a higher rate than seven other Southern California species. Also, the more hairy leaves of *Encelia farinosa* Gray, which are produced under water stress, have been observed to lose water faster on a per unit area basis than larger less hairy leaves that are produced under more favorable moisture conditions (Shreve, 1921). The only major exception to this trend of increasing transpiration with pubescence I have found in the literature is a comparative study by Wood (1934), in which he found that tomentose succulent leaves had very low transpiration rates, but even then he implies that succulence is the important consideration since the observed response was similar to stem succulents without pubescence. These studies suggest that the boundary layer resistance effect on transpiration is not very great.

The results of the second group of experiments in which the indumentum was actually removed show inconsistencies. Haberlandt (1914) measured transpiration from paired leaves of *Stachys lanata* Jacq., one of which had the hairy covering clipped from the upper surface, and found the clipped leaf to lose the more water under both sun and shade conditions. Several investigators (Sayer, 1920; Hendrycy, 1967; and Wuenscher, 1970) have made similar studies with *Verbascum thapsus*. Sayer was unable to detect a difference between shaved and unshaved plants, whereas Hendrycy and Wuenscher reported an increase in water loss when the pubescence was removed. The ambiguity of the results is not entirely unexpected since a basic assumption made by all the authors, i.e. that the boundary layer resistance was the only diffusive resistance affected by removal of the indumentum, is undoubtedly faulty. The main resistance to gas exchange is located at the epidermis proper and depends on the structural and functional characteristics of the stomata and cuticle.

A loss of cuticular waxes and a change in the light environment of the stomata, both of which should be expected to affect the diffusive resistance to water vapor, would almost certainly accompany the removal of a heavy layer of pubescence. This is not to deny the existence of a boundary layer associated with pubescence but to point out that it only makes up a part of the total diffusive resistance, and that in so doing the maximum value it may take will always be less than the total diffusive resistances observed. Thus the comparatively low total resistances (i.e. high transpiration rates) reported for pubescent species in the first group of experiments indicates an even lower boundary layer resistance which must also be essentially constant due to the fixed structure of the indumentum layer. The direct boundary layer effect of pubescence on transpiration is therefore considered to be small in spite of some reports to the contrary (Wuenscher, 1970).

Short Wave Radiation. Pubescence has been further tied to the water economy of plants in an indirect way through energy budget considerations. Plausible mechanisms have been proposed by which pubescence may participate in temperature regulation of transpiring surfaces by either reducing the absorption of radiant energy or by enhancing its dissipation once it has been absorbed. The postulated reduction is believed to result from high reflectance properties. As a rule, the lighter a surface appears, the greater is its reflectance of the visible radiant energy falling upon it. The vegetation of many dry regions have a grayish-white cast because of the high reflectance of dominant pubescent species. Reflectance measurements from a wide variety of plant leaves support the contention that high reflectance of visible radiation is frequently associated with pubescence. Shull (1929), working with wavelengths of radiation between 430–700 nm, found that the thick layer of white hairs on the lower surface of *Populus alba* L. leaves uniformly reflected nearly 50% of the incident energy as compared to 10–20% for non-pubescent plants. Other species measured by him which are known to have rather dense indumenta [*Sassafras variifolium* (Salisb.) Ktze., *Asclepius syriaca* L., and *Arctium minus* (Hill) Bernh.] also showed comparatively high reflectance values. Billings and Morris (1951) made similar measurements but over a broader spectral range (400–1100 nm) and found that the desert species with dense pubescence [*Eurotia lanata* (Pursh) Moq., *Artemisia tridentata* Nutt., *Atriplex lentiformis* (Torr.) Wats. and *Atriplex canescens* (Pursh) Nutt.] showed comparatively high reflectance for visible wavelengths (400–700 nm); the reflectivity beyond the visible from 700–1100 nm was variable among both pubescent and non-pubescent species. Pearman (1966) found a marked reduction in reflectance (350–700 nm) in *Arctotheca nivea* Lewin., a sand dune species, when he removed the indumentum from the upper surface.

Exceptions to the pattern linking pubescence and increased reflectance have been observed in *Verbascum thapsus* (Shull, 1929), *Gynura aurantiaca* DC. (Gausman and Cardenas, 1969), and *Glycine max* L. (Gausman and Cardenas, 1973). These exceptions indicate that a hairy layer alone is not enough to bring about high reflectance but must be associated with additional physical characteristics. Furthermore, it does not necessarily follow, as suggested above, that high reflectance in the visible part of the spectrum means low absorption of incident radiation. Two other factors must be considered. First the transmission properties of the pubescent layers, and second the spectral distribution of the total radiation load. In the first case it is the energy that is not transmitted or reflected that is absorbed and so a consideration of reflection alone is not adequate for determining the energy load. This is apparently the reason for the relatively high absorption co-efficients observed for three densely pubescent species: *Cratystylis conocephala* (F.V.M.) S. Moore., *Olearia pimeloides* (DC.) Benth., and *Kochia sediflora* F.V.M. from the deserts of Australia (Sinclair and Thomas, 1970). In the second case, reflectivity and transmissivity valves for different parts of the spectrum are important because about half of the solar energy falling upon plants lies beyond the visible part of the spectrum, mostly in the near infrared (Gates, 1966).

Long Wave Radiation. Terrestrial radiation of much longer wavelengths (predominately 3,000–25,000 nm with a peak around 10,000 nm) is also an important energy source (Gates, 1962). The temperature—energy absorption relationships of pubescence must therefore consider reflectance properties in this part of the spectrum as well. Measurements in the terrestrial band show reflectance values below 10% for most plant leaves (Gates and Tantraporn, 1952; Wong and Blevin, 1966). Pubescent leaves included in the measurements show differences from the non-pubescent ones, but the results presented in the two reports cited are opposed as to what the difference is. Reflectance values at 10,000 nm for the most pubescent species studied by Gates and Tantraporn (*Verbascum thapsus, Elaeagnus augustifolia* L., *Asclepias syriaca* L., *Helianthus annuus* L., and *Catalpa speciosa* Warder) showed values between 0 and 1.5% as contrasted with 2 to 7% for the non-pubescent types. On the other hand, Wong and Blevin observed for this same wavelength the highest reflectance values (5–9%) among their most pubescent leaves (*Cerastium tomentosum* L., *Agapanthus umbellatus* L'Her., *Atriplex nummularia* Lindl., *Spinifex hirsutus* Labill., and *Gazania* sp.; all others were 5% and lower. A possible explanation for the opposite findings of the two sets of investigators may be found in the methods they used. Specular reflectance was evidently measured by Gates and Tantraporn while the total reflectance (specular plus diffuse) was measured by Wong and Blevin. It seems reasonable that specular reflectance in this part of the spectrum would be reduced by an uneven surface with a roughness having the dimensions of plant hairs while the total reflectance might be increased because of the scattering properties of such a surface. Whatever the case, the absorption properties of plant leaves to terrestrial radiation are important in energy budget considerations and should be investigated in greater detail.

Plant temperatures are coupled to the terrestrial radiation band not only in energy absorption but also in energy dissipation by emission, according to Kirchoff's law (Reifsnyder and Lull, 1965). The association of pubescence with absorptivity and emissivity could have significant effects on plant temperature, and also water loss, in environments with high terrestrial radiation loads. The greatest effect would probably be found in a leaf with a pubescent lower surface showing reduced absorptivity to ground radiation and a smooth upper surface with a high emittance toward the cooler sky.

Pubescence has also been implicated in energy dissipation through conduction and convection. Wolpert (1962) discusses heat transfer from leaves through convection as a function of exposed surface area. He argues that the increase in surface area due to pubescence should be accompanied by a proportional increase in convective energy transfer. The theoretical consideration of this suggestion is complicated by the development of boundary layers when the pubescence becomes dense and by the conduction properties of the hairs themselves whether living or dead. I am not aware of empirical evidence either pointing toward or away from the significance of pubescence in this context.

Many plant processes other than transpiration are affected by temperature. The consequences of temperature modification with respect to some of these (e.g. photosynthesis and respiration) may be just as important to survival under extreme conditions as a reduction in transpiration.

Relationship to Biotic Factors

Predators, parasites and pathogens tax the survival of most plants growing under natural conditions. Since the initial point of contact with such pests is at the plant's surface, the possible involvement of pubescence with mechanisms of defense or resistance is obvious. Early workers suggested the likelihood of such a relationship but the idea fell into disfavor since the results of experiments designed to test the ideas were inconclusive.

Predators. Some of the earliest experiments on predators were conducted using snails noted for having nonselective grazing habits. They were allowed to graze on plants having different amounts of pubescence. In some instances the plants with pubescence were rejected, in others they were first rejected but later eaten, and in still others they were eaten without hesitation (Stahl cited by Uphof, 1962). Similar experiments involving other organisms gave what appeared to the investigators to be equally ambiguous results (Uphof, 1962). The meaning of such experiments is hard to interpret since the results have little or nothing to do with the quality or quantity of grazing pressures with which plant species must cope in their natural habitat. Recently there has been a revival of interest in the role of pubescence as a deterrent to insect herbivores (Johnson, 1968; Levin, 1973). It may be stated indisputably that pubescence can affect the ability of insects to function through both mechanical and chemical mechanisms. Evidence of how the indumentum may function in a mechanical way is graphically demonstrated by the observations of Richardson (1943) and Gilbert (1971). Richardson investigated the mechanism by which bean leaves are able to immobilize bedbugs since they had been reputably used for that purpose with great success in the Balkan countries. He found that wandering bedbugs passing over bean leaves placed bottom side up, became inextricably entangled by the hooked hairs of the lower surface of the bean leaf. No toxic affects were observed and the bedbugs remained trapped until they starved to death. The studies of Gilbert on the interaction between *Passiflora adenopoda* DC. and characteristically predaceous heliconiine butterfly larvae gave similar results but have even greater ecological implications. Larvae from this group of butterflies comprise a major class of herbivores for the genus *Passiflora*, yet the hooked hairs of *P. adenopoda* rendered the larvae tested completely immobile and caused their death by both wounding and starvation. Observations of like nature have been reported for additional species of plants and insects (Johnson, 1953).

Other important mechanical effects may be less dramatic. Agronomists working with at least three major crop plants (wheat, cotton and soybean), have identified significant relationships linking pubescence to insect resistance. Pubescent varieties of wheat having more than 71 trichomes/mm^2 are less used for egg laying by the cereal leaf beetle *Oulema melanopus* L. than the plants with fewer hairs (Gullun et al., 1973). The more pubescent plants also exhibit additional resistance to larval feeding once the eggs are hatched, as is demonstrated by the production of smaller larvae (Ringland and Everson, 1965). The evidence for the negative effect of pubescence on the cereal leaf beetle is convincing enough to stimulate breeding programs for introducing pubescence into other cereal species (McDaniel and Janke, 1973).

Bud pubescence in cotton has been found to be correlated with both reduced oviposition and feeding preference in the boll weevil, *Anthonomus grandis* Boheman. (Stephens, 1959; Wannamaker, 1957). Under field conditions, varieties of cotton with hairy buds were found to have a lower infection rate than those without hairs (Stephens and Lee, 1961). The density of the pubescence seems to be important in determining the degree of resistance. In soybean, resistance to the potato leaf hopper (*Empoasca fabae* Harris.) and the Mexican bean beetle (*Epilachna varivestis* Mulsant.) appears to be more related to the hair orientation and size than to hair density. Broersma et al. (1972) observed that the number of potato leaf hoppers was reduced on plants having erect hairs over those having appressed hairs or no hairs at all. Larvae of the Mexican bean beetle are less successful on plants having long erect trichomes and have been observed to fall off when traversing such leaves (Van Duyn et al., 1972).

The temporal and spatial distribution patterns of plant pubescence in the deciduous forest of eastern North America suggests a long and intertwined coevolutionary relationship with insects. Copious amounts of plant hairs are produced as a covering on the young tender leaves of almost all species. Each year there is a period of one or two weeks in early spring when trichome production encompasses a large fraction of the total metabolic activity in the deciduous forest community. During this period of rapid growth plant hairs account for as much as 50 percent of the increase in leaf dry weight. This flush of trichome growth preceeds the annual bloom of insect predators by a matter of days. Leaves are especially vulnerable to disruptive damage during the early stages of their ontogeny. They frequently fail to develop normally after they have been attacked. Comparatively little damage by insects takes place on young leaves still covered with pubescence (Johnson, 1968). Of special interest in this regard are observations by Feeny (1968) on the timing of tannin production in Oak leaves (*Quercus robur* L.). He found that condensed tannin first appeared in developing leaves in May. This he related to a progressive development of insect resistance. The connection with pubescence lies in the fact that the production of the tannin in Oaks must get underway just at the time the hairs are being shed from the leaf surface (Johnson, 1968). It thus appears that defenses toward insects may shift with age from an obvious mechanical barrier in the case of plant hairs to a chemical one in the case of the tannins.

The role pubescence can play as a physical obstruction to predation is easily seen, but in addition to this there is a more subtle role related to resistance at the biochemical level. Much of what is accepted today concerning the evolution of plant-herbivore interactions involves back and forth adjustments of biochemical pathways (Whittaker and Feeny, 1971). Trichomes are frequently distinctive biochemical compartments containing classes of compounds that may be toxic or offensive to would-be predators. The most obvious examples of this are seen in the stinging hairs found among the plant families *Urticaceae, Euphorbiaceae, Loasaceae,* and *Hydrophyllaceae* (Thurston and Lerston, 1969). Contact exposure with living plants having such hairs has caused the death of horses and perhaps even men. The identity of the chemical compounds responsible for the toxic properties is still a subject of controversy (Thurston and Lerston, 1969).

The chemical relations of non-stinging hairs are also complex. Levin (1973) reviews the possible involvement of glandular trichomes in the biochemical defense against insects. Such trichomes have been shown to contain high concentrations of phenoles and alkaloids. Beckman et al. (1972) surveyed the stem hairs from 39 plant species and concluded that phenolic type compounds were present in large quantities in all but 7. Exudates from the glandular hairs of tomato (*Lycopersicon esculentum* Mill.), one of the species investigated by them in detail, has previously been associated with resistance to cowpea aphids (*Aphis craccivora* Koch.) (Johnson, 1956). Alkaloid compounds are particularly abundant in trichomes of *Nicotiana* and *Petunia* (Thurston et al., 1966; Thurston, 1970). These products were found to be highly toxic to aphids (*Myzus persicae* Sulzer.) and the larvae of tobacco hornworm (*Manduca sexta* Johannson.).

Parasites and Pathogens. The chemical and mechanical characteristics of the indumentum must also have significance with respect to parasitic and non-parasitic algae, fungi, and bacteria that interact at the plant surface. Plant pathologists in the early 1900's suspected the involvement of leaf pubescence and other surface structures in disease resistance (Walker, 1924). Stuart (1906) observed that varieties of potatoes with small pubescent leaves were infected less by potato blight [*Phytophthora infestans* (Mont.) deBary.] than more glabrous types. The resistance was ascribed to the reduction of surface moisture due to the quick drying properties of the hairy covering. Similarly Appel (1951) noted that varieties of raspberries with thick waxy coverings remained free from attack by *Coniothyrium* while other less waxy types were severely infected. He suggested that this difference was related to the more rapid drying after wetting of varieties with waxy surfaces. The idea that pubescence had something to do with disease resistance fell into disfavor in large measure, as the biochemical complexities of the interacting organisms began to emerge (Walker, 1950). Currently the stage is being set for a revival of interest in this area of inquiry, with the recognition of what has been termed the "phyllosphere" (Ruinen, 1961), a term coined to characterize the uniqueness of the leaf surface as an environment for microorganisms. It is now generally recognized that the physical nature of the plant surface will affect the development of microbes in a variety of ways. Much attention is now being given to the structural and chemical variation of the cuticular surface, as witnessed from the reports in the book "Ecology of Leaf Surface Microorganisms" that resulted from an international symposium by the same name (Preece and Dickinson, 1971) and the excellent book entitled "The Cuticles of Plants" by Martin and Juniper (1970). But as yet, little quantitative work has appeared with respect to pubescence in this regard. A notable beginning in this direction, however, is represented by the work of Jennings (1962). His data show relationships between pubescence and decreased infection rates for spur blight [*Didymella applanata* (Niessl.) Sacc.] and grey mold (*Botrytis cinerea* Deb.) in raspberry canes. His study involved a number of genetic crosses which combine genes for pubescence with other factors affording different degrees of tissue resistance. He concluded that over a three-year period the mechanical effects of pubescence had a much greater influence in reducing cane infections from the two pathogens under consideration than did the more internalized mechanisms of tissue resistance. He ascribed this to the effect the hairs have on liquid water and demonstrated with a dye experiment how the pubescent canes shed water more quickly and completely than those without hairs. It must be recognized then that important biophysical factors related to infection rates by pathogens such as water films, humidity, temperature, and the deposition of spores near stomatal openings (Last and Warren, 1972), will be influenced by the quality and quantity of the indumenta. Ecological consequences will be related to the success of establishment of pathogenic and non-pathogenic microbes alike. The host plant may even conceivably be benefited if its surface characteristics favor the accumulation of a microbiota capable of activities such as nitrogen fixation or antibiotic reactions against the host's pathogens (Last and Warren, 1972; Lerston, N.R., 1972).

Relationship to Physiological Controls

The physiological significance of pubescence will be considered both with respect to its role in (1) material exchanges, and (2) metabolic regulation.

Material Exchanges. Trichomes that retain their protoplast for extended periods are frequently involved in either assimilatory or excretory activities. Such activities may include the exchange of water, minerals and/or organic compounds. In the epiphytic members of the Bromeliaceae and Orchidaceae assimilatory scales or trichomes provide a principal pathway for the uptake of water. Studies on the absorbing trichomes of *Tillandsia usneoides* by Dolzmann (1964) provided insight into the relationship between morphological structure and water absorption. He noted the presence of a substance located between the protoplasm and the cell wall that was capable of swelling and storing water. Highly developed mitochondria are associated with the cell membrane where water uptake occurs. Haberlandt (1914) noted that plants with trichomes having pitted walls at their base are likely to be effective in absorbing nocturnal dews.

The opposite response, i.e. water loss from trichomes, has also been noted. This may occur through exudation or by evaporation through the cell wall. Specialized trichomes of *Monarda fistulosa* L. have been observed to extrude up to 450 $\mu m^3$of aqueous solution per minute (Heinrich, 1973). Active transport processes appear to be associated indirectly with the movement of the water. Energy expended in the transport of ions from trichomes helps to establish an osmotic gradient along which water can flow passively toward the trichome surface. Even though it may appear that the principle function of trichomes in such cases is the secretion of organic and inorganic materials (see below), it still may be that this process is an important factor regulating the water status of some plants. Water exudation from specialized trichomes is common among plants of the humid tropics (Haberlandt, 1914). Haberlandt postulated that water lost in this way may enable plants to maintain a proper turgor in the cells, and prevent the accumulation of water in the intercellular spaces of leaves. A "dry" mesophyll could be of significance for insuring satisfactory gas exchange and a resistance to infections from pathogens.

Evaporative water loss from hairs has been studied by Miroslavov (1958) and Woolley (1964). Miroslavov using a dye technique studied cuticular transpiration of living hairs in young shoots of *Melampyrum nemorosum* L., *Euphrazia tatarica* Fisch. and *Veronica longifolia* L., and concluded that more water evaporated from the trichomes than from other epidermal cells. Woolley (1964) noted that the increased transpiration from the surfaces of living trichomes on soybean leaves might seriously tax the water economy of pubescent plants under drought conditions. Such trichomes might also be expected to be sites of water uptake if they are wetted when the turgor of the leaf cells and internal tissues is low.

Material exchanges other than water include both inorganic and organic materials. Such exchanges are perhaps best illustrated by the research on the structure and function of salt glands (Thomson, 1974). Trichomes of various specialized morphological types have been shown to participate in the active transport and regulation of plant salts. It has long been recognized that salt crusts develop on the shoots of some plants growing in saline environments (Haberlandt, 1914). Recent studies on salt secreting plants such as *Tamarix aphylla* Krast. (Thomson et al., 1969), *Atriplex spongiosa* F.V.M. (Osmond et al., 1969), and *Spartina foliosa* Trin. (Levering and Thomson, 1972) indicate that salt deposits may develop in a variety of ways (Thomson, 1974). In the case of *Tamarix,* salt seems to be concentrated by active transport in the small vacuoles of the glandular trichomes. Hydrostatic pressure that develops in the secretory cells forces the salt solution into the walls and extracellular space between the walls and the cuticle and thence through the pores of the cuticle to the plant surface; here the water evaporates leaving the salts behind. In the case of atriplex trichomes, salt is concentrated in the vacuoles of large terminal bladder cells which rupture under hydrostatic pressure. After drying, a mixed surface layer of salt and dead cell materials remain. In *Spartina,* the secretory process involves a large basal cell that exhibits an elaborate system of parallel partitioning membranes that run perpendicular to the leaf surface. The salt is believed to flow along these membrane channels in response to a standing concentration gradient as proposed for some animal transport systems (Levering and Thomson, 1972).

Whatever the mechanism of salt secretion, its result seems to be the maintenance of a rather constant ionic balance in the plant body. The concentration of salts in the trichomes and the fluid they secrete is almost always higher than that of the soil solution or of the underlying plant tissue (Berry, 1970). If the salt environment of the roots is changed, i.e., increased, decreased or shifted in ionic species, the secreted fluid tends to change in the same direction while the stem and leaf mesophyll remain constant (Thomson, 1974). It is easy to see how this kind of osmotic regulation could be of great significance to plants in saline environments.

A wide variety of organic compounds are secreted and stored by plant trichomes (Uphof, 1962). Glandular secretions may be in the form of proteolitic enzymes, polysaccharides, sugars, organic acids, waxes, oils, resins, etc.

(Luttge, 1971). It appears that the mode of secretion is through the action of dictyosomes, as observed in the secretion of mucilage by the trichomes of *Rumex alpinus* L., *R. maximus* Schreb., and *Rheum rhabarbarum* L. (Schneph, 1968). The contributions of such secretions to the welfare of the plant have been interpreted in terms of waste elimination, protective devices and even as attractants to beneficial organisms (Luttge, 1971).

Metabolic Regulation. A more direct physiological role has been suggested for phenolic type compounds observed in the trichomes of many species by Beckman et al. (1972). They concluded that such compounds tend to be concentrated in granular bodies that appear in the terminal portions of trichomes but that in response to certain stimuli, e.g., light, this material may be dissipated quickly by moving into the epidermal cells. They argue that phenols are not only involved in defense mechanisms but also in wound-healing and in the general synthesis and regulation of the important growth hormone indoleacetic acid. Such arguments are compatible with those of Robinson (1974) concerning alkaloids. He concludes that "never again should anyone say that alkaloids are inert end products of metabolism", since they are actively broken down and reconstituted systematically in specific patterns related to developmental stages.

Conclusive evidence on the physiological roles of active compounds such as the alkaloids in the trichomes of *Nicotiana,* or the hallucinogen in marijuana (*Cannabis sativa* L.) localized in the glandular hairs of the flowering bract (Hammond and Mahlberg, 1973), is still unavailable.

CONCLUSIONS

Information contributing to an understanding of the ecological and evolutionary significance of plant pubescence comes from both observational and experimental studies. The multitude of papers in the literature that testify to the high frequency and complexity of trichomes and pubescence throughout the plant world provide overwhelming evidence that strong selection forces are operative in the development of indumenta. Such observations do not provide definitive answers as to what the selective forces might be, but have furnished the base for many teleological interpretations. Good experimental data defining the effect of pubescence on the processes that couple the plant to its environment are rather sparse in comparison. Attempts at quantitative studies have emphasized the physical environment over the biotic and to a large extent have centered around water relations. Efforts to gain support for the generalized teleological interpretation concerning the role of pubescence as a significant deterrent to transpiration have been generally unsuccessful. It is no longer tenable to consider the reduction of transpiration as a primary function of plant hairs; such a view is much too simplistic. Rather, the consequences of pubescence need to be considered at all contact points along the plant-environment interface.

In view of the complexity exhibited by trichomes and pubescence, it should not be surprising that seemingly contradictory results appear in the literature. It is entirely reasonable that in some cases trichomes may retard transpiration through a boundary layer effect while in others they may increase it by participating as an additional evaporative surface.

The most important point needing emphasis in this regard is that all physical exchanges involving energy and matter that take place at the plant surface must involve the indumentum when one is present.

The relationship with the biotic environment should be expected to show even more apparent inconsistances. Current theory concerning co-evolution for organisms that interact antagonistically postulates a seesaw adjustment syndrome, in which first one gains the advantage and then the other. What this means in the case of pubescence with respect to predators and pathogens is that in some cases pubescence might appear as a deterrent while in others it would be an attractant, depending on which way the evolutionary balance has shifted. Thus, observations by Ross (1933) on the pubescence-foraging sawfly (*Sterictiphora apios* Ross.) serve as evidence that pubescence and insects have had a long history of interaction. The mouth parts of the sawfly appear to have become modified to accommodate the harvest of leaf hairs of the ground bean, *Apios tuberosa* Moench. To quote Ross, "the scythe-shaped mandibles are used in the cutting operation. The sawfly, when feeding, stands at one point, crops the pubescence in front of it in a semicircular swathe, then steps forward and repeats the process until the leaf is denuded." This relationship is the extreme opposite of that reported by Gilbert (1971), in which pubescence of *Passiflora adenopoda* completely immobilized and caused the starvation death of a particular group of potential predators. These extremes can easily be accommodated by evolutionary theory and in fact should be considered as dramatic evidence of the ongoing interaction between plant pubescence and the biotic environment.

The involvement of glandular trichomes in the movement and regulation of important organic and inorganic materials, as has been shown, further extends the probable ways that pubescence may have adaptive significance. But here also a full spectrum of variation might be expected. In some instances the indumentum appears to function as a tissue system quite independent of other plant tissues as was noted by Cannon (1908).

It now seems clear that the ecological and evolutionary significance of pubescence must be queried from a multifaceted stance. No longer can pubescence be considered as a simple adaptation to arid environments. Its complex development must have come about in response to a whole host of environmental and developmental factors. Clues as to its functional roles can be obtained by deciphering patterns of occurrence with respect to where and when it is found. But the mechanism by which more efficient function is achieved must be worked out thoroughly before its occurrence is accepted as an adaptive adjustment to a particular stress.

ZUSAMMENFASSUNG

Die Kenntnisse, die zum Verständnis der ökologischen und evolutionären Bedeutung der Pflanzenbehaarung beitragen, werden sowohl durch Beobachtungen als auch durch experimentelle Studien gewonnen. Die grosse

Anzahl von veröffentlichten Studien, die das häufige Vorkommen und die Verwicklung von Trichomen und Behaarung in der Pflanzenwelt bestätigen, liefern überzeugenden Beweis dafür, dass erhebliche Selektionskräfte in der Entwicklung von Indumenten am Werk sind. Solche Beobachtungen geben aber keine genaue Auskunft über das Wesen dieser Selektionskräfte; sie bilden jedoch die Grundlage für zahlreiche teleologische Deutungen. Im Vergleich dazu sind gute experimentelle Daten, welche die Wirkung der Behaarung auf die Vorgänge zwischen der Pflanze und ihrer Umwelt definieren, ziemlich selten. Quantitative Studien haben die physische Umwelt anstatt der biotischen Umwelt betont, und beschäftigen sich hauptsächlich mit Wasserverhältnissen. Versuche, Interesse zu erwecken für die allgemeine teleologische Deutungen der Rolle, die die Behaarung in der wichtigen Hemmung der Transpiration spielt, waren im allgemeinen erfolglos. Die Verminderung der Transpiration kann nicht mehr als Hauptfunktion der Pflanzenhaare angesehen werden; eine solche Ansicht ist viel zu simplistisch. Statt dessen müssen die Auswirkungen der Behaarung an allen Kontaktpunkten zwischen Pflanze und Umwelt in Erwägung gezogen werden.

In Anbetracht der Vielfalt von Trichomen und Pflanzenbehaarung sollte es kaum zu verwundern sein, dass scheinbar widersprüchliche Ergebnisse in der einschlägigen Literatur erscheinen. Es ist durchaus zu erwarten, dass in einigen Fällen die Trichomen die Transpiration durch einen Grenzschichteffekt verzögern, während sie in anderen Fällen die Transpiration steigern, indem sie als zusätzliche Verdunstungsoberfläche wirken.

Der wichtigste Punkt, der hier betont werden soll, ist die Tatsache, dass in allen physikalischen Prozessen an der Pflanzenoberfläche, bei denen Energie und Masse eine Rolle spielen, das Indument berücksichtigt werden muss, insoweit eines vorhanden ist.

Es ist zu erwarten, dass das Verhältnis zu der biotischen Umwelt noch offensichtlichere Widersprüche aufweist. Die zirkulierende Theorie der Ko-Evolution von Organismen mit antagonistischer Wechselwirkung postuliert ein wippenartiges Regulierungssyndrom, in dem zuerst der eine Organismus überhand nimmt und dann der andere. Dies bedeutet, dass die Behaarung in einigen Fällen als Abschreckungsmittel gegen Beutetiere und Pathogene wirkt, während sie in anderen Fällen eine anziehende Wirkung ausübt, je nachdem, wohin sich das evolutionäre Gleichgewicht verschoben hat. So zeigen Beobachtungen von Ross (1933) an der Behaarungs-vertilgenden Sägefliege (*Sterictiphora apios,* Ross), dass Behaarung und Insekten eine lange Beeinflussung aufeinander ausübten. Die Mundteile der Sägefliege scheinen dem Verzehren der Blatthaare der *Apios tuberosa* (Moench) angepasst worden zu sein. Nach Ross: "Die sichelförmigen Kinnladen werden im Schneideprozess angewandt. Beim Fressen steht die Sägefliege an einem gewissen Punkt, verzehrt die Behaarung in einem halbkreisförmigen Bogen um sich herum, bewegt sich dann vorwärts und wiederholt denselben Vorgang." Dieses Verhältnis ist genau das Gegenteil dessen, was Gilbert (1971) über die Behaarung der *Passiflora adenopoda* (DC.) berichtet, die die vollkommene Erstarrung und Verhungern einer gewissen Gruppe von potentiellen Beutetieren hervorrief. Diese Extreme können beide von der Evolutionstheorie berücksichtigt werden und liefern einen dramatischen Beweis für die andauernde Wechselwirkung zwischen Pflanzenbehaarung und der biotischen Umwelt.

Die Rolle von Drüsentrichomen in der Bewegung und Regulierung wichtiger organischer und anorganischer Stoffe erhöht die Möglichkeit adaptiver Bedeutung der Pflanzenbehaarung. Hier ist ebenso ein ganzes Spektrum von Variationsmöglichkeiten zu erwarten. In einigen Fällen scheint sich das Indument als Gewebesystem völlig unabhängig von anderen Pflanzengeweben zu verhalten, wie Cannon feststellte (1908).

Es scheint also klar, dass die ökologische und evolutionäre Bedeutung der Pflanzenbehaarung von einem vielseitigen Standpunkt aus betrachtet werden muss. Die Behaarung kann nicht mehr als einfache Adaption an eine trockene Umwelt angesehen werden. Ihre komplizierte Entwicklung muss durch eine ganze Reihe von Umwelt- und Entwicklungsfaktoren beeinflusst worden sein. Andeutungen ihrer Funktionsrolle entstehen bei der Untersuchung der Frage, wann und wo sie auftritt. Der Mechanismus jedoch, durch den eine erfolgreichere Funktion erzielt werden könnte, muss erst gründlich ausgearbeitet werden, ehe ihr Auftreten als Angleichung an einen besonderen Umweltfaktor angenommen werden kann.

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