

Some Functional Aspects of Angiosperm Pollen

Sangtae Lee

(Department of Biology, Sung Kyun Kwan University, Suwon 440-746, Korea)

被子植物花粉의 機能形態學的 小考

李 相 泰

(成均館大學校 生物學科)

Abstract

Some studies conducted by the author were reviewed to explain the significance of pollen diversity in pollen size, exine thickness, aperture type and number, and wall stratification. A factor analysis study of 18 pollen and anthecological characters implied that the pollen size is affected by the style length, and the pollen size in turn is positively related with the exine thickness for a mechanical support and with the aperture number for the pollen hydration on the stigma. The measurement of pollen dehydration showed a tendency in which pollen grains, regardless of their morphology, are dehydrated within five minutes and maintain an equilibrium. This suggested that pollen is highly drought-resistant and unlikely to develop any specific modification to prevent the pollen desiccation. A harmomegathic study demonstrated that oblate and prolate grains tend to become spherical after they are hydrated and implied that colpus is advantageous for the harmomegathy only if it is associated with the prolate shape. The measurement of hydration time through aperture vs. exine wall exhibited that the exine wall also functions as a water conducting route and suggested that the evolutionary trend of exine from the tectate to the intectate is to facilitate a pollen hydration.

Introduction

Diversity of the angiosperm pollen has been recognized since last century. Much attention has been paid to the functional and adaptive aspects of the highly complex pollen wall. Some of the functions suggested early by Wodehouse(1936) were that aperture plays a role as a

pollen tube exit and a harmomegathy, the accomodation of volumetric changes when pollen is dehydrated and rehydrated. There were many papers to support these aspects (Payne, 1972; Heslop-Harrison, 1977, 1987; Kress, et al., 1978; Thanikaimoni, 1986). Payne(1981) and Blackmore and others (Blackmore, 1982; Blackmore & Barnes, 1986; Scotland, et al., 1989) showed that the exine and surface structures are sure to facilitate the harmomegathy as well. Heslop-Harrison(1976) and others found out that the chambered exine, that is characteristic of so many angiosperms, serves as the repository for tapetum-derived incompatibility proteins. The exine-held materials also include some sticky substances which make the pollen grains possible to be sticked to the pollinators as well as to the stigma surface (Hesse, 1979). Recently, Dickinson and colleages (Elleman & Dickinson, 1986; Sarker, et al., 1988). demonstrated that the proteins reserved in the exine cavity react with those of stigma to create continuity between contact of the papilla wall and the grain protoplast and the pollen hydration is facilitated.

In spite of many works, the adaptive significance of most pollen features is not yet known. In other words, it still remains uncertain why pollen grains are so diverse in terms of grain size and shape, aperture type, number and arrangement, exine stratification, surface sculpturing pattern, etc. As Stebbins(1974, p. 292) pointed out, "this lack of understanding is due largely to the complexity of the problem and the paucity of information on a comparative basis."

In relation to this problem, I want to review some of my works I pursued firstly to see the independent sets of correlations among pollen and anthecological characters by a factor analysis (Lee, 1978); secondly to see the relationships between the pollen dehydration to the morphology, and the pollen shape change according to their grains shape and aperture type (Lee, 1977); and thirdly to see the hydration through aperture vs. exine wall in conjunction with the exine stratification (Lee, 1988).

Factor analysis study

The complex variables of pollen diversity and pollination systems might usefully be analyzed by multivariate statistics. Factor analysis is one of such statistical technique for reducing a large number of variables to a small number of hypothetical factors. These factors are often biologically interpretable because they summarize the predominant trends of correlated character variations and thus identify subgroups of functionally related characters (Seal, 1968). Employment of factor analysis seems appropriate for this study in which I have attempted to isolate subgroups of inter-related pollen and anthecological characters and to discover possible causal factors responsible for these correlations (Sokal & Rholf, 1969).

A total of 100 species of angiosperms were randomly chosen only if all of their pollen and anthecological (i.e., ecological, pollination, and floral) characters are available. Eight pollen and 9 anthecological characters were measured or coded. Table 1 is the matrix of five

Table 1. Factor loadings, communalities and eigenvalues obtained by factor analysis of 17 characters from 100 species of various angiosperm families.

Character	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Communality
Grain length	.89166*	-.10949	-.51627*	.09072	-.42890	.90818
Grain width	.87859*	.18220	-.43906	.01369	-.45420	.90873
Equatorial shape	-.05333	.75824*	.26561	-.02005	-.12330	.61898
Aperature number	.31320	.04708	-.12756	.08480	-.71770*	.55116
Exine thickness	.68326*	-.00406	-.18096	.05151	-.64567*	.72528
Sculpture pattern	.41985	-.12196	-.32360	-.05472	.07064	.24713
Pore width	.38247	.05444	-.03593	.19794	-.14612	.17841
Colpus length	.04725	-.65715*	-.16463	-.07488	.46592	.58944
Vector size	.54528*	-.34845	-.54975*	.26618	.07287	.59268
Floral type	.11042	-.06499	-.04513	.70163*	-.04254	.51235
Temperature	-.26344	-.48504	.30658	-.03254	-.00987	.39673
Stigma surface	-.28198	.76370*	.08987	-.11159	.04907	.68352
Stigma shape	.19673	.53323*	.08964	.38926	-.18908	.44279
Style length	.59570*	.07030	-.82282*	.47681	.00924	.99702
Flower width	.38234	-.10424	-.92613*	-.22641	-.10422	.91764
Flower length	.44371	-.02381	-.87206*	.32083	-.01018	.89122
Orifice width	.14987	-.26069	-.69936*	-.61334*	.04093	.85719
Eigenvalue	5.00654	2.54217	1.56308	1.40021	0.51539	

* Factor loadings that are considered biologically important within each factor.

factors extracted from the data. Each of the factors is characterized by several characters with high absolute values of factor loading, namely, the importance of the characters in each factor. In distinguishing "high" factor loading, 0.5 was arbitrarily adopted as the standard since by this criterion a biologically interpretable set of characters appears to be sorted for each factor.

Factor 1 is characterized by high loadings of grain length, grain width, exine thickness, vector size and style length. Thus factor 1 represents the size relationships among pollen, style, and vector. In other words, a relationship is revealed in which large grains tend to possess thick exine and are associated with flowers possessing long styles that are pollinated by large animals.

Factor 2 is characterized by high loadings of equatorial shape, colpus length, stigma surface and stigma shape. This factor denotes a relationship in which the oblate grains tend to possess short colpi and such grains associate with flowers bearing roughened and branched stigmas such as of wind-pollinated plants.

Factor 3 shows high negative loadings of grains length, vector size, style length, flower width and length, and orifice width. This factor reveals somewhat similar relationship to that of factor 1. The relationship of flower size characters is emphasized. Pollen size is related to vector size as well as to flower size.

Factor 4 shows high loadings in floral type and orifice width. The correlation indicates that tubular or zygomorphic flowers tend to have a narrower orifice. This factor will be ignored, however, because no pollen characters have a high factor loading.

Factor 5 shows high loadings in aperture number and exine thickness. The tendency demonstrated here is that grains with thick exine have many apertures.

The relationships extracted from the factor analysis exhibited that many pollen characters are interrelated as well as correlated with floral characters, especially with the style length.

The first positive relationship I want to discuss is that between pollen size and style length (Table 2), that is, the longer-styled species tends to have larger grains. The floral sizes are also strongly related to pollen size but less strongly than the style length to it. This suggests

Table 2. Correlation coefficient matrix of characters associated with the floral biology of angiosperms.

Cha.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	—	.967	-.179	.492	.718	.304	.277	.100	.541	.099	-.268	-.292	.134	.592	.531	.501	.315
2	.907	—	.132	.456	.694	.279	.357	-.146	.413	-.004	-.335	-.080	.210	.531	.479	.451	.269
3	-.179	.132	—	-.012	.028	-.191	.115	-.508	-.410	-.090	-.322	.584	.308	-.146	-.228	-.163	-.291
4	.492	.456	-.012	—	.536	.035	.107	-.303	.074	.062	-.033	-.082	.128	.174	.201	.176	.024
5	.718	.694	.028	.536	—	.279	.293	-.193	.242	.073	-.088	-.262	.192	.268	.276	.212	.146
6	.304	.279	-.191	.035	.279	—	.153	.166	.267	-.132	-.191	-.247	.039	.338	.315	.312	.227
7	.277	.357	.115	.107	.293	.153	—	-.118	.224	.102	.032	-.093	.095	.224	.049	.151	-.138
8	.100	-.146	-.508	-.303	-.193	.166	-.118	—	.281	.071	.267	-.425	-.412	.028	.078	.102	.255
9	.541	.413	-.410	.074	.242	.267	.224	.281	—	.213	-.080	-.391	-.079	.664	.459	.562	.243
10	.099	-.004	-.090	.062	.073	-.132	.102	.071	.213	—	-.071	-.206	.209	.349	-.102	.308	-.347
11	-.268	-.335	-.322	-.033	-.088	-.191	.032	.267	-.080	-.071	—	-.331	-.270	-.354	-.277	-.256	-.126
12	-.292	-.080	.584	-.082	-.262	-.247	-.093	-.425	-.391	-.206	-.331	—	.361	-.072	-.109	-.084	-.097
13	.134	.210	.308	.128	.192	.039	.095	-.412	-.079	.209	-.270	.361	—	.237	-.153	.073	-.386
14	.592	.531	-.146	.174	.268	.338	.224	.028	.664	.349	-.354	-.072	.237	—	.674	.918	.248
15	.531	.479	-.228	.201	.276	.315	.049	.078	.459	-.102	-.277	-.109	-.153	.674	—	.760	.762
16	.501	.451	-.163	.176	.212	.312	.151	.102	.562	.308	-.256	-.084	.073	.918	.760	—	.402
17	.315	.269	-.291	.024	.146	.227	-.138	.255	.243	-.347	-.126	-.097	-.386	.248	.762	.402	—

Determinant of correlation matrix = 0.0000007 (0.661629831D-06)

Cha. = Character; 1. Grain length; 2. Grain width; 3. Equatorial shape; 4. Aperture number; 5. Exine thickness; 6. Sculpture pattern; 7. Pore width; 8. Colpus length; 9. Vector size; 10. Flower type; 11. Temperature; 12. Stigma surface; 13. Stigma shape; 14. Style length; 15. Flower width; 16. Flower length; 17. Orifice width.

that pollen size is strongly influenced by the style length and less directly by the other flower sizes and pollinator size. One biological implication of this relationship is that large pollen grains might contain enough stored energy to support pollen tube growth down to a long style and that small grains would be sufficient for pollen tube growth through short styles (Pandey, 1973; Dulberger, 1975; Taylor & Levin, 1975).

The relationship among the grain size, exine thickness, and aperture number might be interpreted as a mechanical function on one hand and a hydration function on another. Mechanical resistance of the pollen grain is essential and the grains with large size and many apertures would be natural to possess a thick exine. The mechanical aspects of the exine has been thoroughly reviewed by Bolick (1981). The second point was the hydration function of this relationship. The thick exine might make difficult for the pollen to be hydrated because the apertural part would transfer water more readily than the exine. The larger the grain size, the more aperture would be required for faster pollen hydration. This function has been dealt by Heslop-Harrison (1979a,b, 1987), however, there has been no good experimental evidence provided. A well known evolutionary trend is that the more advanced plants show a higher number of apertures and a tendency of change from colpus to pore. The most significant function of the former evolutionary trend I assumed is that the increase in aperture number may be favored for a rapid pollen hydration from the stigma. I tried to pursue this problem and the result will be presented later.

Now how about the relationship between grain shape and aperture type? The tendency of prolate grains to have a long colpus but oblate ones to have pores is not surprising. Let's look at this relationship just little more detail. Table 3 shows that the W/L ratio is significantly greater in the porate grains than in the colpate or colporate grains. In other words, porate grains tend toward an oblate shape and coplate grains toward a prolate shape. Payne (1972) showed that the colpus and pore have different harmomegathic patterns, that is, as a dry pollen is hydrated, the colpus expands in width and shortens in length, whereas a pore swells without expanding the diameter. However, attention has rarely been paid to the significance of this association between grains shape and aperture type. I would like to propose that this association is functionally important. If the colpus were associated with spherical or oblate

Table 3. Comparison of pollen shapes in terms of width/length ratio between three different types of apertures.

Aperature types	No. of species	Width/length ratio		Test	
				t-value	Significance
Colpate	26	.92 ± .19	>	1.50	n.s.
Colporate	34	.98 ± .17	>	3.66	P<0.01
Porate	35	1.19 ± .29			

grains, it would be unable to expand in width as occurs in prolate grains because the exine wall is somewhat solid and not-expandable, instead, the whole exine wall tends towards a spherical shape. Colpi which lie mostly perpendicular to the polar axis would be advantageous in the prolate grains, but disadvantageous in the spherical and oblate grains where the solid shell of the wall would not allow the expansion of the colpus in width. An important point here is that the functional association between the aperture type and the grain shape may have been instrumental in the evolution from colpus to pore. There was a relatively high correlation of the grain shape with the stigma shape and type of wind- vs. insect-pollinated flowers. I don't know if or how this association is functionally meaningful at this moment. At any rate, if the spherical or oblate shapes are favored in nature for any reason, the colpus would not function well and its advantage as a harmomegathic device would be lost. This relationship between the aperture type and harmomegathy was observed and will be discussed later.

Dehydration and harmomegathic experiments

An assumption they can easily make is that harmomegathy might facilitate to prevent the pollen dessication and help the pollen hydration. It seems to be important not to loose water before the pollen grains land on the stigma. I made a quartz-fiber balance to measure the change of pllen weight after taking out the grains from the anther. Figure 1 is the diagram of the

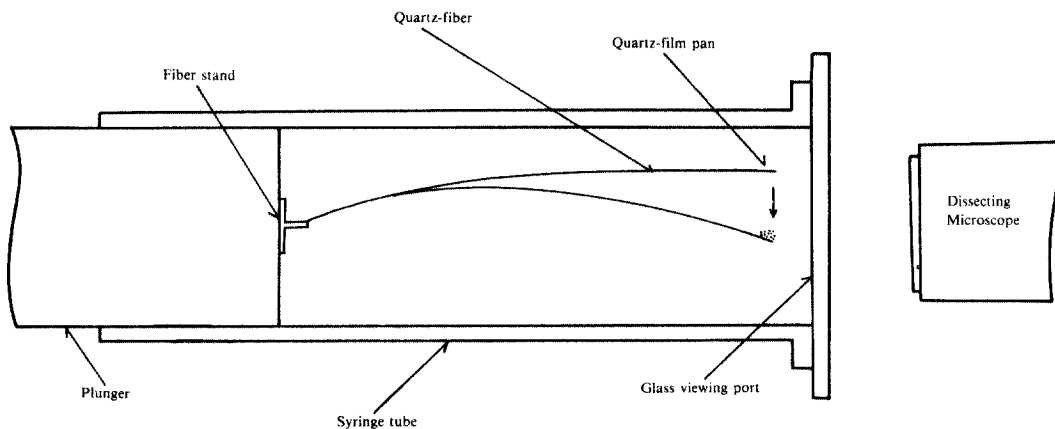


Fig. 1. Quartz-fiber micro-balance. Modified syringe tube anchored horizontally on stand. Vertical displacement of quartz fiber measured with dissecting microscope outfitted with an ocular micrometer. Scale: 1.25x.

quartz-fiber balance. Pollen grains taken from the fully matured but undeheated anther, were transferred onto the pan of the quartz fiber tip with an eyelash brush. The distance of the pan movement was measured with a stereomicroscope which was installed in front of the

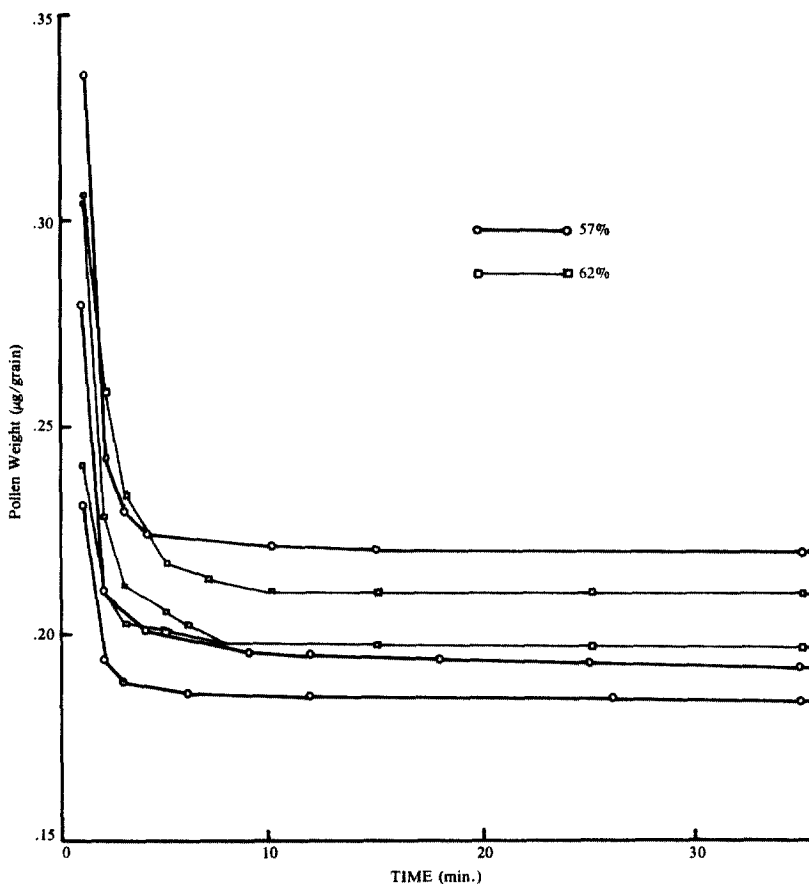


Fig. 2. Rate of water loss of pollen in *Lonicera japonica* in two different humidity conditions.

window of the balance body.

Figure 2 shows a repeatability of the measurement in which several measurements of weight change in the *Lonicera japonica* pollen show almost the same pattern of dehydration. Figure 3 is the graph of pollen weight change through time of 24 species. The result of the weight change was compared with pollen characters such as size, shape, aperture type and number, etc. However, I didn't find any correlation between them. Instead, an important point noticed was that pollen grains whatever their morphology is, loose water in a very short time, within about five minutes, and maintain an equilibrium thereafter. Since the pollen grains might be fully viable even after the time of equilibrium, it seemed that the pollen grains might have obtained an ability for a drought-resistance in their early evolutionary history. It would be possible to conclude, therefore, that aperture types would not do anything to prevent the pollen dessication and the pollen grains might not need any device to maintain water at a certain level at least on the point of pollen morphology.

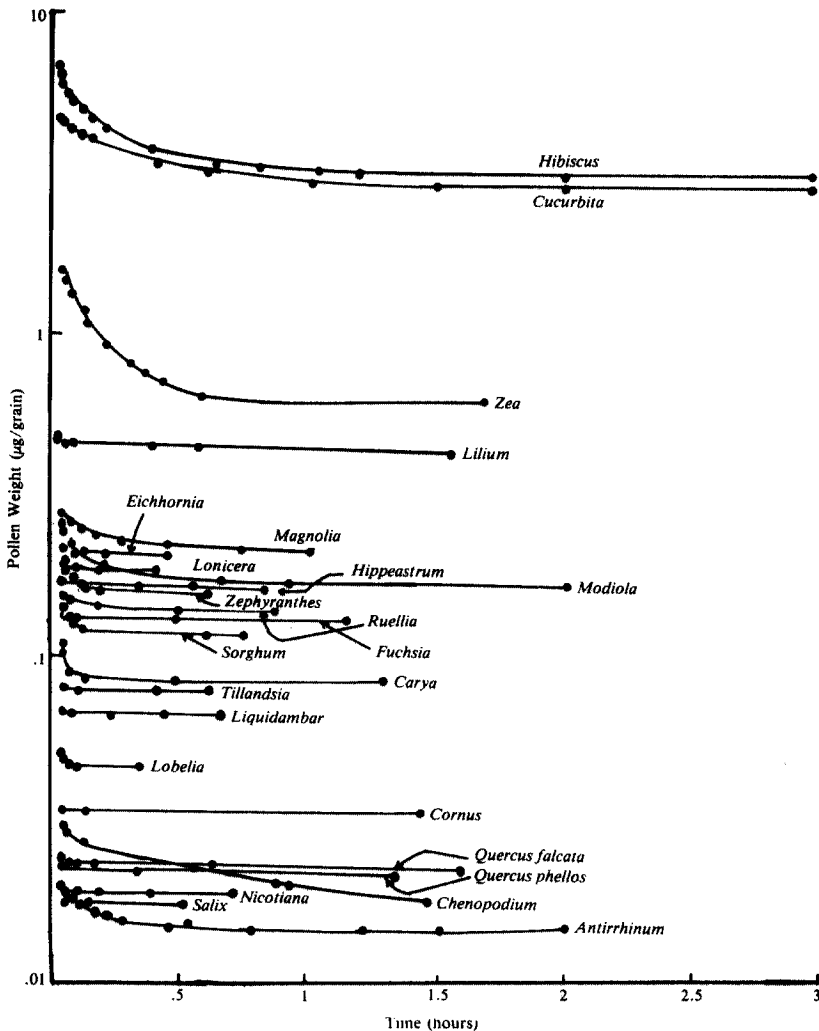


Fig. 3. Rate of water loss of pollen in different species as measured by change in weight. Note: pollen weight is in the log scale.

The harmomegathic pattern shown by observing the dry grains and the wet grains which were hydrated in the culture medium (Payne, 1972), was the same as expected. The colpus widened in width and the pore remained the same in size. After the measurement of their size, I plotted them on the graph (Fig. 4). As you well notice, all the grains become or at least tend to become spherical after they are hydrated. If oblate and spherical grains have colpi, the colpi might not be advantageous for harmomegathy at all. Pollen shape would be therefore a possible factor influencing the evolution of aperture from colpus to pore, as mentioned the above.

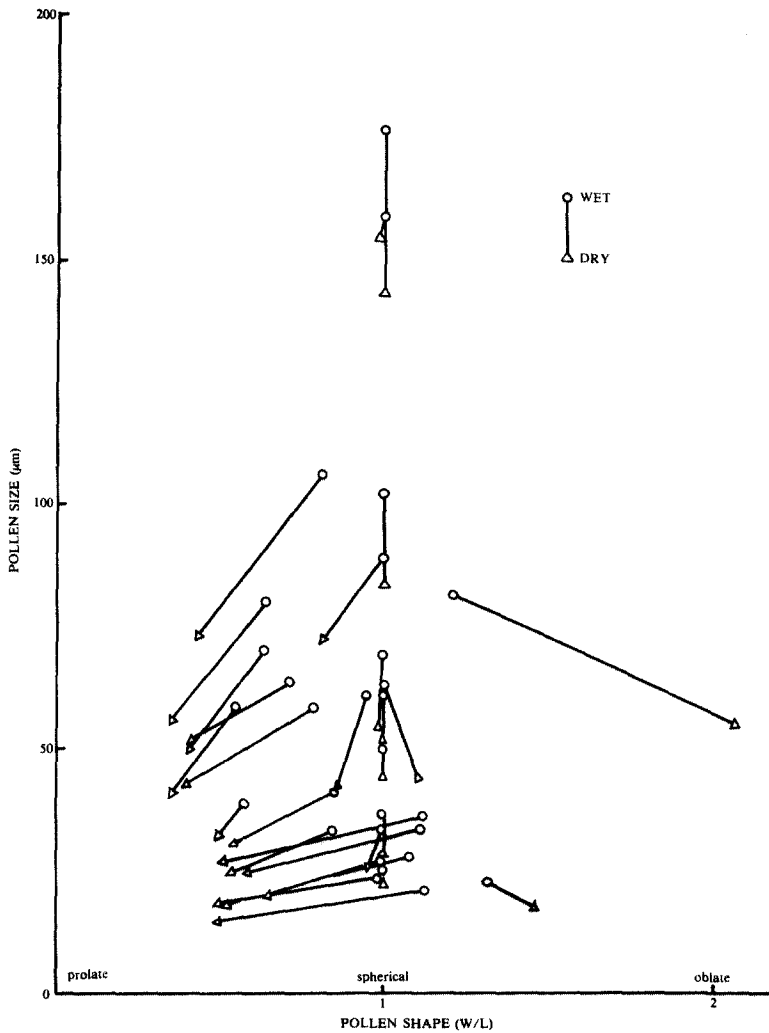


Fig. 4. Change of pollen shape according to water loss and absorption of different pollen grains.

Hydration through aperture vs. exine wall

I measured hydration time through aperture vs. exine wall of different species by orienting the grain axis parallel and perpendicular to the stigmatic surface. This observation was made under a light microscope ($\times 100$). But the adjustment of the pollen orientation was tricky and the measurement of the hydration time was not so easy under such a low magnification, and more elaborate studies need to be made for the verification (Lee, 1988).

The hydration time and frequency from 15 species were measured. The preliminary result

Table 4. Measurement of stigmatic fluid absorption of various pollen grains which were artificially deposited on the stigma

Aperture type Specific name	Pollen volume*	Orient. contact	Absorption time (min.)	No. of grains absorb/not absorb	
MONOSULCATE					
<i>Magnolia liliflora</i>	23.4	equator	10-(20)-60	10	2
		pole	15-140	4	3
<i>Liriope platyphylla</i>	11.2	equator	25-(35)-90	20	1
		pole	35-(40)-100	10	0
<i>Scilla scilloides</i>	13.7	equator	50-210	10	8
		pole	40-180	2	6
TRICOLPORATE					
<i>Cornus alba</i>	6.2	equator	50-(100)-140	15	0
		pole	110	2	5
<i>C. officinalis</i>	5.2	equator	5-(20)-120	91	0
		pole	120	2	15
<i>Forsythia koreana</i>	11.0	equator	1-(3)-14	29	0
		pole	2(14)-20	31	0
<i>Lagerstroemia indica</i>	8.6	equator	100-165	5	4
		pole	135-195	7	6
<i>Ligustrum obtusifolium</i>	12.9	equator	60-(80)-180	19	0
		pole	70-170	7	7
TRIPORATE					
<i>Dunbaria villosa</i>	106.4	any	60-(100)-140	12	8
<i>Elaeagnus umbellata</i>	20.6	equator	10-(20)-60	18	0
		pole	25	1	4
<i>Oenothera odorata</i>	273.5	equator	5-(20)-60	15	9
		pole	5-(20)-40	7	2
PERIPORATE					
<i>Calystegia japonica</i>	181.1	any	75-(100)-200	17	5
<i>Dianthus sinensis</i>	47.1	any	50-(75)-100	13	4
<i>Hibiscus syriacus</i>	134.0	any	50-(100)-165	13	13
<i>Quamoclit angulata</i>	140.0	any	70-(110)-115	13	6

* Volume unit $\times 1000\mu\text{m}^3$.

was summarized in Table 4. The hydration time was variable in different species between 1 to 200 minutes as well as within the same species. I compared the hydration time between the different orientations of each species as well as the hydration time to the pollen characters such as pollen volume and aperture type.

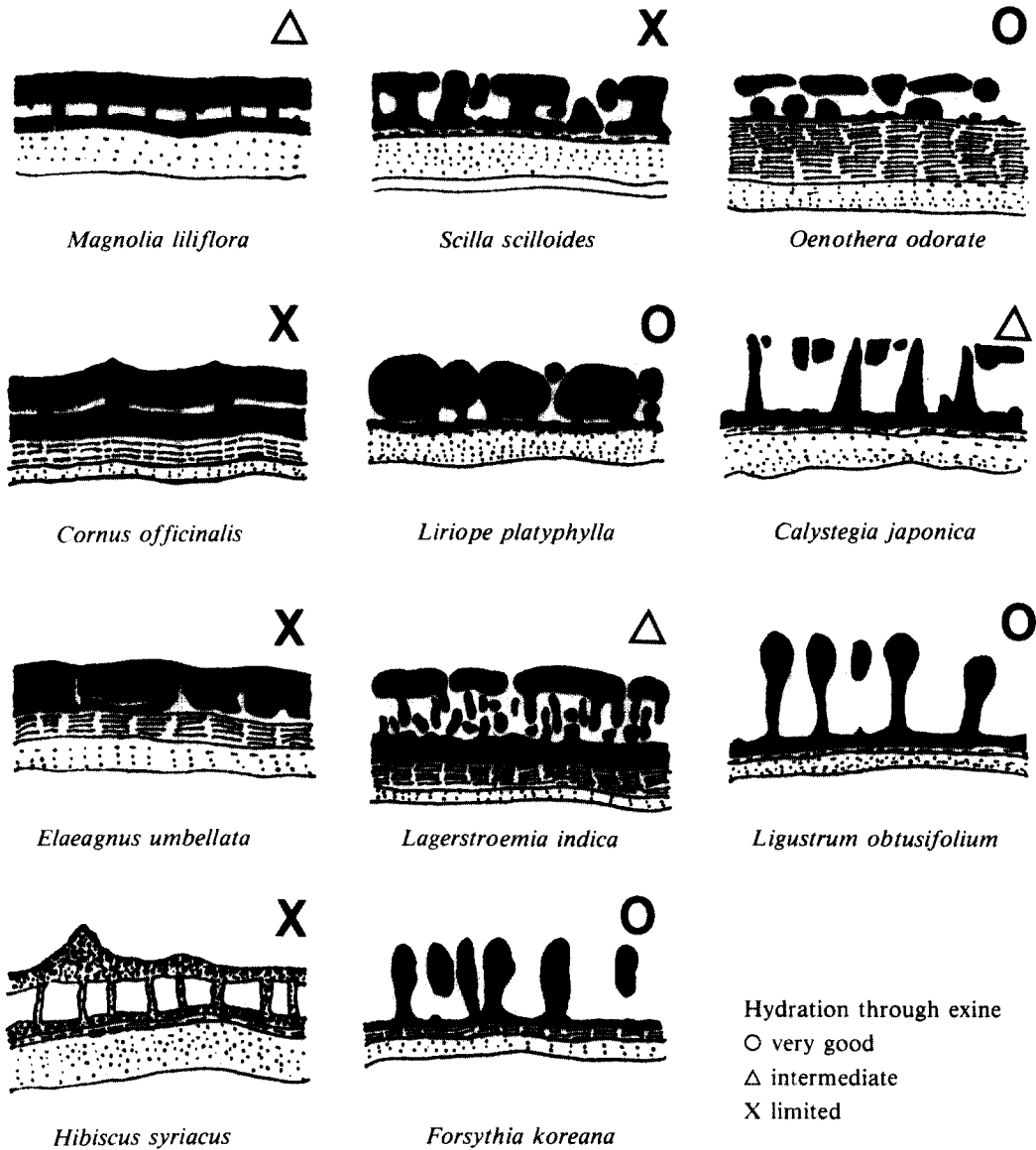


Fig. 5. Diagrammatized exine stratification and the data of hydration experiment. There is a strong tendency in which the exine an open tectum transfers water more freely than that with a closed tectum.

I found no significant correlation between hydration time and such pollen characters but I could have found that the times between aperture and exine are not much different from each other in some species such as *Liriope platyphylla*, *Oenothera odorata*, *Lagerstroemia indica*, whereas the hydration through aperture was faster than that through exine is *For-*

sythia koreana, and the hydration through exine was almost impossible in *Cornus officinalis*. This result was compared with the exine stratification. Figure 5 shows the diagramatized TEM photographs along with the summarized hydration data. Here, sign O depicts that the hydration through exine is very good, X limited, and Δ intermediate. As you may see, there is a good correlation between the exine stratification and the hydration time through exine. Namely, as the tectum is more widely open or intectate, there is a strong tendency of hydration through exine. This datum is still preliminary and needs to be supplemented, however, the result well supports the Heslop-Harrison's hydraulic scheme (Heslop-Harrison, 1979b). Moreover, the evolutionary trend of exine stratification from tectate, semitectate and to intectate (Walker & Skvarla, 1975) is possible to be functionally interpreted. The wide variation of the measurements might also imply there are many factors involved in pollen hydration such as self-incompatibility interaction (Sarker, et al., 1988), degree of contactness, dry or wet nature of stigmatic surface, and so on (Heslop-Harrison, 1987). It is believed that more works are necessary to be made for understanding and elucidating the pollen functions.

摘 要

花粉의 크기, 表壁의 두께, 發芽口의 數, 表壁의 層狀構造등의 花粉多樣性에 대한 機能的 意義를 本人의 論文數編을 綜說함으로서 說明하였다. 花粉 및 開花生態學的 特徵 18가지의 要因分析으로부터 花粉의 크기는 花柱의 길이에 影響을 받으며, 花粉의 크기는 機械的 支持를 위해 表壁의 두께와 花粉吸水를 위해 發芽口의 數와 陽의 聯關關係를 보임이 示唆되었다. 大部分의 花粉은 그들의 形態와 無關하게 5分內에 물을 잃고 平衡狀態에 이르는 것으로 보아 상당히 乾燥抵抗性이 크며 脫水를 막기 위한 形態의 特殊化는 찾지 못하였다. 花粉이 吸水후 長球形이나 短球形으로부터 球形으로 변하는 傾向을 보이는 것은 溝口가 長球形과 聯關되어 있을 때만 變形能에 도움이 됨을 暗示케 하였다. 花粉의 發芽口와 表面을 통한 吸水測定은 表壁도 吸水通路로서 重要하며 全覆性에서 無覆性으로의 表壁의 進化는 花粉吸水를 위한 것임을 支持해 주었다.

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