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reduced to the level presumably present in the cellulose cultures until after 46 days. The prolonged effect of glucose at levels below those detectable suggests that glucose inhibits enzyme synthesis at high concentrations and regulates it at low concentrations. We postulate that the level of soluble carbon compounds such as glucose may regulate microbial cellulase synthesis on cellulose. As soluble carbon sources are depleted, cellulase is synthesized until an equilibrium becomes established between synthesis and inhibition of synthesis by the products of hydrolysis. The establishment of a static, maximum enzyme level in the cellulose cultures exemplifies this situation. The cellulose source presumably contains only low levels of soluble carbohydrates. Thus, little inhibition of synthesis is exercised and cellulase synthesis proceeds rapidly. As enzyme concentration increases, more soluble hydrolysis products become available to the fungus and inhibitory effects eventually create an equilibrium between synthesis and enzyme degradation.

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Androhermaphrodites of *Lychnis Alba*

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Abstract. Lychnis alba was found to produce four categories of flowers; i.e. pistillate, staminate, gynohermaphrodite and androhermaphrodite. Hermaphrodites are formed when a rudimentary pistil (pistillodium) or stamens (staminodea) develop into mature organs on the ovaries of otherwise pistillate or staminate flowers. Androhermaphrodites, in particular, were studied and their structure and behavior found to be essentially similar to corresponding parts of regular staminate and pistillate flowers. Ovaries of androhermaphrodite flowers exhibited variations in style number ranging from one to five. Ovaries with two to five styles were self- or cross-fertile with any good *Lychnis alba* pollen. One-styled ovaries of androhermaphrodite flowers were of unusual interest because they occurred so commonly, showed a range of development from a pistillodium to a mature ovary, and because they were characteristically self- and cross-sterile.

Lychnis alba Mill. (Caryophyllaceae) is dioecious with definite pistillate flowers on one plant and definite staminate flowers on a separate one. However, it appears that the dioecious habit is

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not yet completely established in this species. Typical pistillate flowers have a ring of rudimentary stamens (staminodea) encircling the base of the ovary, while typical staminate flowers have a rudimentary pistil (pistillodium) projecting centrally from the basal portion of the flower. When these rudimentary stamens or pistils develop into mature organs, hermaphrodite flowers result. When a pistillate flower develops stamens, it then may be called a gynohermaphrodite flower. Similarly, when a staminate flower develops a pistil, it then may be called an androhermaphrodite flower. The flowers of *Lychnis alba* may thus be grouped into four categories on the basis of their sexual expression.

1. Pistillate. This flower typically contains a well developed compound pistil with five styles (Fig. 1). Pistillate plants were found to produce pistillate flowers only and never an occasional hermaphrodite.

2. Staminate. The flower typically contains ten fertile stamens (Fig. 2). True staminate plants produce staminate flowers only and never an occasional hermaphrodite.

3. Gynohermaphrodite. Produced on what appear to be otherwise normal pistillate plants, this flower has stamens and a compound pistil essentially the same as that found in regular pistillate flowers (Fig. 3). Gynohermaphrodite flowers, only, were produced by these plants. All the stamens in each of several hundred gynohermaphrodite flowers examined by Dean (1) were sterile.

4. Androhermaphrodites. Produced on what appear to be otherwise normal staminate plants, this flower has stamens and a pistil, but the pistil is typically smaller than those found in regular pistillate flowers (Fig. 4). Androhermaphrodite flowers occur mixed on the same plant with other flowers which externally appear to be identical to true staminate flowers.

The purpose of this paper is to report upon hermaphrodite plants, and, in particular, androhermaphrodites of *Lychnis alba* found in outdoor plots and among plants grown in a greenhouse from seed. This paper will also describe the morphology and anatomy of androhermaphordite flowers and compare their structure with that of typical pistillate and staminate flowers of this plant.

MATERIALS AND METHODS

The first androhermaphrodite plant found (plant #20, Table 1) appeared in a lot of twenty-nine plants grown in a greenhouse (2). Additional androhermaphrodites were found during examinations of large outdoor plots of *Lychnis alba* and were transplanted into a greenhouse. More androhermaphrodites appeared following interbreeding experiments, and others were found among plants grown from seeds collected outdoors. More than fifty androhermaphrodites were available at various times, and of these, fifteen were selected at random for this study.

Plants M-1 and M-2 were found in a West Liberty, Iowa, plot and transplanted into a greenhouse. Plants numbered 8, 10, 11, 13, and 17 were grown from seeds obtained by selfing a two-styled androhermaphrodite flower on plant #20. Twenty-nine seeds resulted and twenty-six plants were produced from them including 12 pistillate, 2 staminate, and the 5 indicated androhermaphrodites. Seven plants remained in the rosette stage and did not flower.

A flower from a normal pistillate plant was pollinated by pollen from a one-styled androhermaphrodite flower from plant #20. A total of 224 seeds resulted, of which 100 were planted. Seventy-three seedlings appeared, and 51 grew to maturity. Among these were 45 pistillate, 4 staminate, and 2 androhermaphrodites (M-8 and M-9).

Another selfed 2-styled androhermaphrodite flower on plant #20 produced 27 seeds. Seventeen plants resulted including 12 pistillate, 3 staminate, and 2 androhermaphrodites (one of which became plant M-3).

Plants M-4 and M-5 appeared in a large lot of plants grown from seeds collected near West Liberty, Iowa. Plants M-6 and M-7 were found among plants grown from seeds obtained by selfing a 2-styled androhermaphrodite flower on plant #13.

Collections of androhermaphrodite flowers from the above plants were made at regular intervals during the period from October, 1959, to July, 1961. Flowers were collected daily from each individual plant throughout at least one flowering period, and records were kept of the style number of every flower collected (Table 1).

Lychnis alba is perennial; new shoots arise outdoors each spring and thereafter throughout the summer from numerous buds on the rootstock. Greenhouse plants cut back to ground level behave similarly. Several androhermaphrodite plants were cut back to the ground after the first flowering period, and new shoots, representing a second season of growth, were allowed to develop. Flowers from a second and, in some cases, a third season of growth were collected, and their style numbers incorporated in Table 1. Since the results for each plant were essentially the same as those obtained during the first growth period, separate tabulations are not given for these later collections. All plants were provided with a 14-hour winter day length

Table 1. Flowering record of individual androhermaphrodite plants.

	20**	M-1	M-2	8*	10**	11**	13**	17	M-3	M-4	M-5	M-6	M-7	M-8	M-9	Total
Male Flowers	2754	926	1067	208	1458	341	270	667	95	99	56	48	7	873	388	9257
Style number of Androhermaphrodite Flowers																
0 Styles	5	0	0	0	0	2	0	0	0	0	0	0	0	0	0	7
1 Style	356	37	215	92	91	114	90	2	2	19	1	3	2	213	9	1246
2 Styles	320	3	146	169	122	230	148	2	1	22	0	5	4	238	12	1422
3 Styles	33	0	11	17	26	53	40	0	0	2	0	0	1	38	1	222
4 Styles	0	0	0	0	1	6	2	0	0	0	0	0	0	6	0	15
5 Styles	1	0	1	0	0	3	0	0	0	0	0	0	0	1	0	6
Total Number Flowers	3469	966	1440	486	1698	749	550	671	98	142	57	56	14	1369	410	12175
Total Number Androhermaphrodite Flowers	715	40	373	278	240	408	280	4	3	43	1	8	7	496	22	2918
% Androhermaphrodite Flowers	20.6	4.17	25.9	57.2	14.3	54.6	50.9	.597	3.06	30.2	1.76	14.3	50.0	36.2	5.37	24.0

* Includes second growth period.

** Includes second and third growth periods.

by using incandescent electric lights as supplemental illumination.

RESULTS

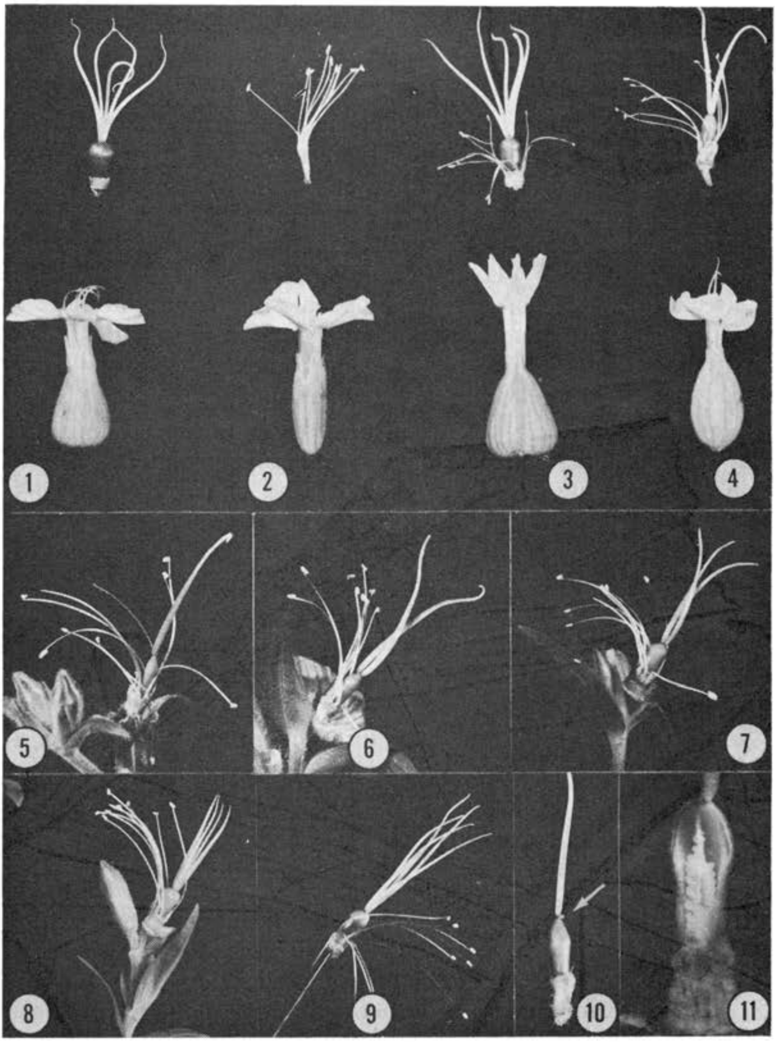
Ovaries of various *Lychnis alba* androhermaphrodite flowers bore styles ranging from one to five in number (Figs. 5-9). From the fifteen plants chosen for individual study, 12,175 flowers were collected for examination. Of this number 1,246 (10.2%) of the ovaries had one style, 1,422 (11.6%) had two styles, 222 (1.8%) had three styles, 15 (.1%) had four styles and 6 (.04%) had five styles (Table 1). The percentage of male hermaphrodite flowers produced by individual plants ranged from a low of 0.597% on one plant (17) to a high of 57.2% on another (8). No plant produced male hermaphrodite flowers exclusively.

Male hermaphrodite plants in most cases produced considerably more staminate flowers than androhermaphrodites. This was true of plants number 10, 17 and 20 and of plants M-3, M-4, M-5, M-6, M-8 and M-9. However, three plants (8, 11, and 13) produced more androhermaphrodite flowers than staminate. One plant (M-7) produced the same number of androhermaphrodite flowers as it did staminate. It should be noted, however, that this was not a vigorous plant and produced a total of only fourteen flowers, a much lower number than for any other plant studied.

Flowers were collected daily for each of the fifteen experimental plants throughout at least one flowering period. Subsequent collections later were made from plants 10, 11, 13 and 20 during each of three additional flowering periods. Similar collections were made from plant #8 during two later flowering periods. In each instance the number of androhermaphrodite flowers produced by an individual plant during any one growing season was found to be essentially the same as that produced during any previous or succeeding flowering period. In no case did the total number of androhermaphrodite flowers produced vary more than 2% from any one flowering period to another.

Close observation of a number of different plants for a period of several weeks, showed that there was no spatial relationship in the production of hermaphrodite flowers. No one branch produced hermaphrodite flowers exclusively. Nor were they more likely to occur on one branch than any other. Occasionally, however, several or all of the flowers on one branch were found to be hermaphrodites. These might or might not have the same number of styles.

During a six day plant-by-plant inventory of one large plot of *Lychnis alba* extending approximately 800 feet along the South side of highway No. 6 about one-tenth mile outside the East



Figures 1-11. Figure 1. Regular pistillate flower of *Lychnis alba*. Figure 2. Regular staminate flower. Figure 3. Gynohermaphrodite flower. Figure 4. Androhermaphrodite flower. Figures 5-9. Series of androhermaphrodite flowers showing ovaries bearing styles ranging from 1-5, (Figs. 1-9, ¾ natural size). Fig. 10. Ovary of 1-styled androhermaphrodite flower showing protuberance (arrow), X 1.5. Fig. 11. Longitudinal section of fresh 1-styled ovary showing sharply-pointed placenta tip, X 2.5.

City Limits of West Liberty, Iowa, regular staminate and pistillate plants were found almost exclusively. However, nine gynohermaphrodite and two androhermaphrodite plants were found. A rough estimate of the number of hermaphrodite plants occurring in the above population as compared with the number of regular staminate and pistillate plants in this plot may be expressed by the following ratios: gynohermaphrodites 1:200

(0.5%); androhermaphrodites 1:900 (0.11%). If flowers only are considered, 241 gynohermaphrodites (5.8%) were found in a total of 4,142 pistillate flowers collected from this same plot (1, 2). Androhermaphrodites would not be expected to appear in this count since pistillate flowers, only, were collected during this time.

Before describing the ovaries of androhermaphrodite flowers, an abbreviated account will be given of the structure of a typical ovary from a five-styled pistillate flower as outlined by Dean (1). A young five-styled ovary of *Lychnis alba* has five carpels, five locules, five placental vascular strands, ten paired strands of stigmatoid tissue, and five carpellary septa (partitions) connecting the inner ovary wall to the central placental column. Placentation in a young ovary is thus axile. In older ovaries (Fig. 17) the septa disintegrate prior to anthesis. The central placental column thus detached from the ovary wall becomes an apparent free-central placenta in a now unilocular ovary.

Five equally spaced, radially arranged (in cross section) vascular strands extend lengthwise throughout the placenta .Vascular strands branching from the placental bundles pass into the ovules. Ten strands of spongy pollen tube conducting (stigmatoid) tissue are equally spaced at the periphery and extend the length of the placental column. The strands of stigmatoid tissue over-arch as the placental apex and unite into a short column connecting the placenta to the ovary roof. Continuing through the ovary roof, the stigmatoid tissue separates into five strands, each entering and extending throughout the length of a style. A single vascular bundle passes from the ovary wall into each style.

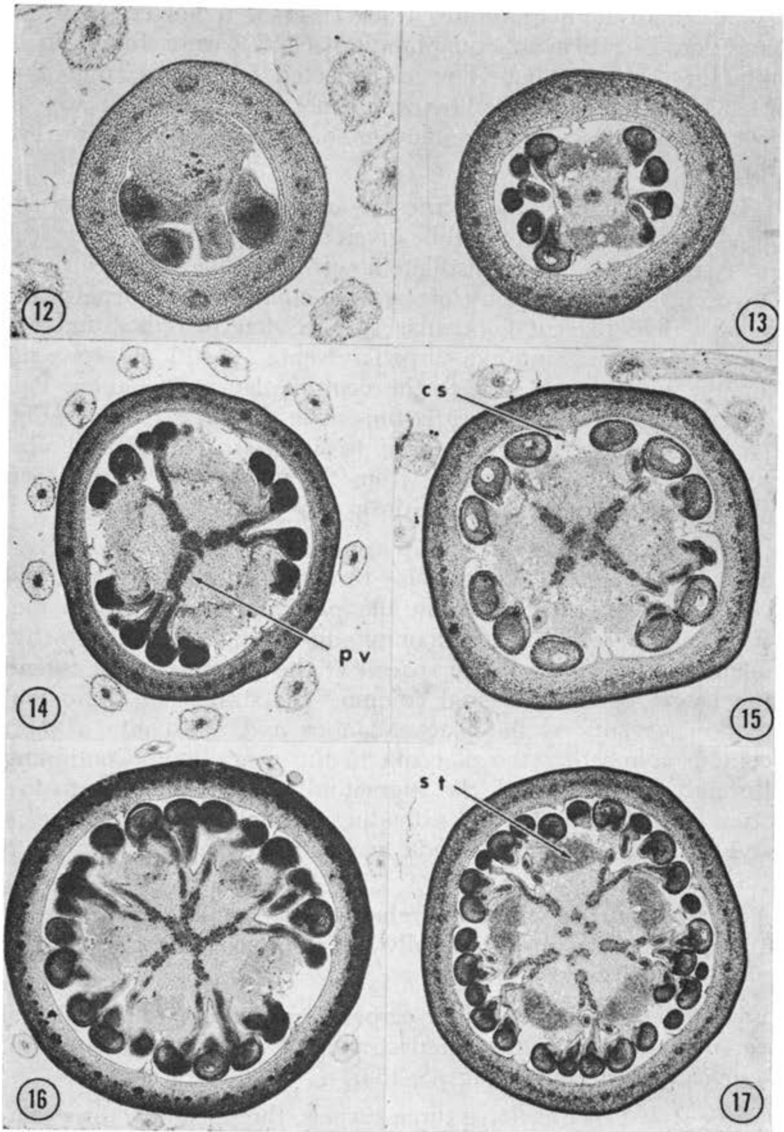
Ovaries of five-styled androhermaphrodite flowers (Figs. 9, 16) have a structure essentially the same as five-styled ovaries of pistillate flowers.

Four-styled ovaries have four carpels, four locules, four placental vascular strands, eight paired strands of stigmatoid tissue, and four carpellary septa (Figs. 8, 15).

Three-styled ovaries have three carpels, three locules, three placental vascular strands, six paired strands of stigmatoid tissue, and three carpellary septa (Figs. 7, 14).

Two-styled ovaries have two carpels, two locules, two placental strands, four paired strands of stigmatoid tissue, and two carpellary septa (Figs. 6, 13).

The placentae of all ovaries described above are axile in young flowers, but become free-central when the carpellary septa disintegrate before anthesis.



Figures 12-17. (pv, placental vascular bundle; st, stigmatoid tissue; cs, carpellary septum). Figure 13. Same, 2-styled ovary. Figure 14. Same, 3-styled flower. Figure 13. Same, 2-styled ovary. Figure 14. Same, 3-styled ovary. Figure 15. Same, 4-styled ovary. Figure 16. Same, 5-styled ovary. Figure 17. Cross section of 5-styled ovary of regular pistillate flower. (Figures 12-15, X 22; Figures. 15-17, X 12).

Typical one-styled ovaries have one carpel, one locule, one carpellary septum, two strands of stigmatoid tissue, and one strand of placental vascular tissue (Figs. 5, 12). Placentation in a young one-styled ovary appears submarginal (3). The placenta later becomes free-central when the single carpellary septum disintegrates to free the placenta from the ovary wall.

Matured one-styled ovaries of androhermaphrodite flowers were roughly cigar-shaped with a laterally bent apex terminating in a small two-parted protuberance (Fig. 10). The single style arises near the end of the bent ovary tip. Perhaps the two-parted protuberance represents the stigmatic margins of the single carpel which failed to fuse completely at the ovary apex. This may be equivalent of the two-parted stigmatic crest of primitive angiosperm taxa (3). The lateral protuberance was found to be a constant feature of all one-styled ovaries of both pistillate (1) and androhermaphrodite flowers.

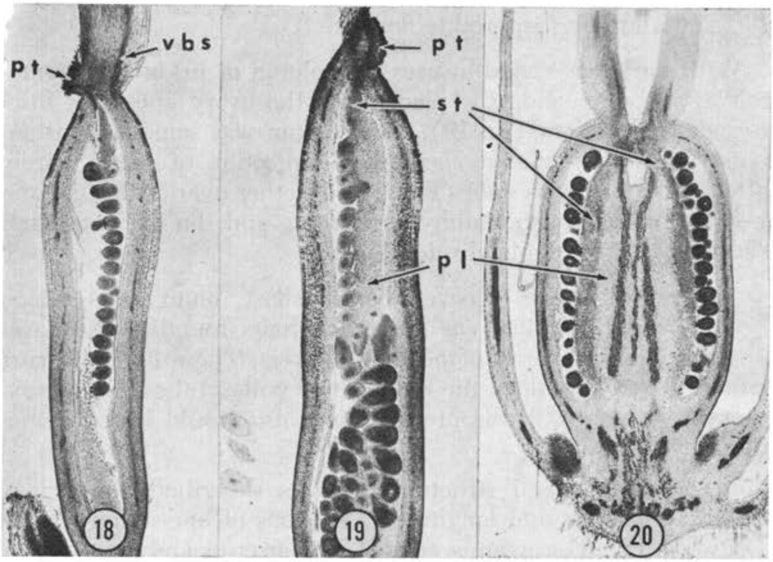
With some one-styled ovaries the column or bridge of stigmatoid tissue connecting the placenta to the ovary apex was fully formed and intact (Fig. 19). This column was sometimes attenuated at the tip into a needle-like projection of tissue barely attached to the ovary roof (Fig. 11). In other ovaries this column was variously broken, stubby, or lacking, and the placenta itself shortened or incompletely developed.

The protuberance is covered with short, blunt hairs which become highly lignified, as do similar hairs found at the bases of the styles on ovaries of pistillate flowers. These lignified hairs would effectively block the entrance of pollen tubes. Stigmatoid tissue terminating in the protuberance also would be non-functional.

Some of the general structural features described above may be noted in cross and longitudinal sections of one-styled ovaries (Figs. 12, 18, 19) as compared with similar cross and longitudinal sections of ovaries from a five-styled pistillate flower (Figs. 17, 20).

During several series of pollination experiments with numerous androhermaphrodite flowers, it was found that any ovary with two to five styles was fertile and produced viable seeds when self- or cross-pollinated by any good *Lychnis alba* pollen. However, practically all one-styled ovaries were sterile under similar conditions. Forty, one-styled ovaries were both self- and cross-pollinated during this study. Most of the pollen was known to be good, because it was used concurrently on other ovaries of pistillate flowers which subsequently produced viable seeds. All but one one-styled ovary failed to produce seeds or exhibit any other visible sign (i.e. swollen ovary) of successful pollination. The one fertile and productive one-styled ovary produced seven seeds. Only three plants resulted from these seeds, two staminate and one pistillate.

Straining reactions with iron-aceto-carmine and numerous pollination experiments indicate a considerable but variable degree of sterility of the pollen in nearly all anthers from androhermaphrodite flowers. However, except for one plant, enough pollen was fertile so that these plants were able to serve as the pollen parent in a number of experimental crosses. The one exception to this was plant M-9, in which the pollen of all androhermaphrodite flowers produced by it was completely sterile when placed upon its own or any other *Lychnis alba* pistils. Iron-aceto-carmine reactions indicated that all the pollen was bad and much of it was badly deformed.



Figures 18-20. (pt, protuberance; pl, placenta; st, stigmatoid tissue). Figures 18-19. Longitudinal sections of 1-styled ovaries of androhermaphrodite flowers, X 9.5 and 10. Figure 20. Longitudinal section of 5-styled ovary of regular pistillate flower, X 7.

Considering all factors, however, the main reason for the sterility of one-styled ovaries seems to be the premature breakage or malformation of the column of stigmatoid tissue which ordinarily extends intact from the placental tip upward through the ovary roof into the style.

As previously stated, a hair-like rudimentary pistil or pistillodium occurs centrally in the basal portion of each staminate flower of *Lychnis alba* (Fig. 21,a). Many ovaries of one-styled androhermaphrodite flowers had partially formed pistils, each of which had undoubtedly developed from a pistillodium. A complete series (Fig. 21,b-m) of these imperfectly formed one-styled ovaries, representing various stages in development from a pistillodium to a full-sized and typical one-styled ovary, was

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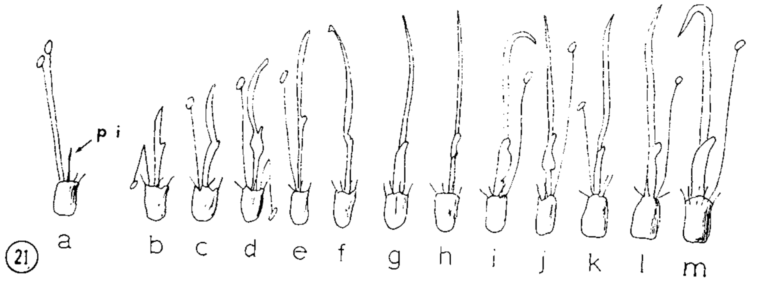

Figure 21. a-m. (pi, pistillodium). a .Floral parts removed from staminate flower to show pistillodium. b-m. Showing various stages in the probable development of a 1-styled ovary from a pistillodium.

repeatedly found. Incompletely developed ovaries showed no evidence of ovules, except for tiny, brown, granular appearing bodies found occasionally in larger specimens. Partially developed ovaries were not included in Table 1.

Discussion

Although *Lychnis alba* is described as a dioecious species with distinct pistillate and staminate flowers, it appears that the dioecious habit is not yet fully established, as evidenced by the constant occurrence of a pistillodium in staminate flowers and of staminodea in the pistillate. When these rudimentary structures mature, hermaphrodite flowers result.

Many phylogenists believe that the bisexual or hermaphrodite condition is primitive in the flowering plants, and that dioecism has been derived independently in the families where it is now found, apparently in the majority of cases at the species level. Dioecism is not always clear cut or well established. Allen (4) pointed out that most mutations affecting the sex genes in hermaphroditic species will tend towards unisexuality, but that most mutations in dioecious species will tend toward hermaphroditism or monoecism, or phylogenetically backwards. This latter trend is perhaps a reflection of the incomplete establishment of dioecism in the majority of such plants.

Ovaries of androhermaphrodite flowers bearing styles ranging from two to five in number were similar in structure to ovaries of pistillate flowers having a corresponding number of styles. However, it was the one-styled ovaries of androhermaphrodite flowers which proved to be of unexpected interest because of the large percentage of androhermaphrodite flowers having one style (10.2%), the fact that they were characteristically self- and cross-sterile, and that a complete range in size and degree of development from a rudimentary pistil only slightly larger and more complex in structure than a pistillodium to a fully developed pistil was repeatedly found (Fig. 21,a-m).

Two styled ovaries were found in somewhat greater numbers but were similar in structure and behavior to ovaries with higher style numbers.

The androhermaphrodites used in this study were determined to be diploid but beyond this cytological observations were not made, nor were experiments conducted attempting to explain the occurrence of androhermaphrodites in *Lychnis alba.* However, in this connection the following brief comments are pertinent.

Westergaard (5) summarized the literature concerning the influence of the X and Y-chromosomes and the autosomes in sex-determination in *Lychnis* (*Melandrium*) *alba.* His paper should be consulted for a good account of these and related topics which are too lengthy to be given here. Warmke and Blakeslee (6) and Westergaard (7), working independently with artificially derived polyploid *Lychnis* (*Melandrium*) *alba* plants, conclusively proved that the Y-chromosome was definitely larger (6.2μ) than the X (4.4μ) or the largest autosome (2.8μ). Both men showed the Y-chromosome to be a powerful and decisive factor in sex-determination for this dioecious species. When a diploid *Lychnis alba* plant has two X-chromosomes (XX) it is pistillate or female. When a Y-chromosome is present (XY) a staminate or male plant results.

Westergaard (5) noted that the sex-determining influence of a single, unfragmented Y-chromosome was strong enough to suppress the female potentials of three X-chromosomes plus four sets of autosomes (4A+XXXY). Three different regions, each associated with a gene or blocks of genes, appear to be located on the Y-chromosome. One terminal segment suppresses the formation of female sex organs, the other terminal segment controls the final stages in anther development, while the third and middle segment governs the iniation of anther formation. As Westergaard (5) stated, ". . . the Y-chromosome in *Melandrium* determines the sex through complete linkage between genes (or a gene), which suppresses female development and genes which initiate and complete anther development."

Previous writers using the term "hermaphrodite" have not always clearly stated what type or kind was meant, and positive identification as gynohermaphrodite or androhermaphrodite was not made. Westergaard (5) expressed one concept of an androhermaphrodite by calling it a plant with the first flower hermaphroditic but with all subsequent flowers male. The plants described as androhermaphrodites in the present paper do not satisfy this criterion. Some produced a first flower which was androhermaphroditic, but most did not. All, however, produced androhermaphrodite flowers at intervals throughout their entire flowering period.

Flowers collected in Iowa and Minnesota and designated as gynohermaphrodites all had sterile stamens. If this condition should prove true in other geographic areas and with other races of *Lychnis alba,* then the "hermaphrodites" of earlier writers probably were androhermaphrodites and not gynohermaphrodites since they would better fit the results obtained by selfing and crossing experiments which produced viable seeds. It is probable that androhermaphrodites of *Lychnis alba* have not been found and reported more frequently simply because they have not been searched for specifically and thus have escaped all except accidental discovery.

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Influence of Aggregate Size on Soil Moisture Retention[1]

P. M. TAMBOLI, W. E. LARSON AND M. AMEMIYA[2]

Abstract: Soil aggregates ranging from 0.5 to 9.5 mm. in diameter from Nicollet silt loam were used to study the effect of aggregate size on soil moisture retention. It was concluded that (a) between suctions of 0.10 and 1.0 bar, the gravimetric percent moisture retained by various sized aggregates was in the following order: $0.5 < 1.0 < 2.0 \leqslant 3.0 \leqslant 5.0 \leqslant 9.5$ mm.; (b) between suctions of 1.0 and 5.0 bars, the gravimetric percent moisture retained was in the following order: $0.5 < 1.0 \leqslant 2.0 \leqslant 3.0 \leqslant 5.0 \leqslant 9.5$ mm.; and (c) at suction of 10 and 15 bars, the moisture retained by aggregates of various sizes was essentially the same.

Aggregation of particles within the soil mass imparts a characteristic structure to the soil. Both secondary and primary aggregates have been recognized within the soil (1). Secondary aggregates are generally stable when gently sieved in the dry state but usually are not stable when agitated in water. Primary

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