at Marthasville, Hermann, Ashland, and Winfield, Mo. The following collections, available in many of the larger herbaria, represent material essentially similar to that which we studied cytologically: *Eggert*, St. Louis, Mo.; *Davis*, no. 3604, Hannibal, Missouri; *Eggert*, Hematite, Mo.; *Palmer*, no. 34,802, Pontiac, Missouri.

In general aspect *T. pilosa* is entirely different from any other Missouri Tradescantia. The stem is tall and zig-zag, the entire plant is sparingly pilose. The flowering season is late (July to August). The ovary bears long scattered hairs with relatively small glands at their tips. (Fig. 1). The chromosome numbers of 4 plants were determined; as reported in Table 1. All were tetraploids (2n = 24).

A COMPARISON OF VARIATION IN DIPLOID AND TETRAPLOID SPECIES

As has been reported above, *T. reflexa* (in Missouri, Illinois, Wisconsin, and western Michigan) was found to be a tetraploid species. *T. bracteata*, on the other hand, was a diploid. That is, *T. bracteata* like most normal animals and plants had its chromosomes in sets of twos. Those of *T. reflexa* on the other hand, were in sets of fours. This tetraploid condition should have a very marked effect upon the nature of individual differences in the two species. It should increase not only the proportion of intermediates but the number of intermediate types. An example may make this more clear.

Let us consider the simplest possible case, a single factor difference, albinism, for example, as it might be expected to operate in the diploid *T. bracteata*, on the one hand, and in the tetraploid, *T. reflexa* on the other. The inheritance of albinism in Tradescantia, so far as we know, has not actually been studied but the circumstantial evidence from forms existing in nature is all in accord with the hypothesis that as in practically all other flowering plants it is due to a single recessive gene. If we represent the gene for albinism by a, and its normal allelomorph by A, an albino plant of *T. bracteata* will be of the genetical composition (aa) and a pure-breeding full-colored plant will be (AA). Crossing the two will give us a heterozygous F_1 (Aa) which, selfed or crossed *inter se*, will produce the familiar ¼(AA) ½(Aa) ¼(aa) in the second generation. That is, in the diploid species, as regards the gene for albinism, there can be only three possible genetic types, the pure albino (aa) the pure-breeding normal (AA) and the heterozygote (Aa).

In the tetraploid *T. reflexa*, on the other hand, a pure albino must have a gene for albinism in each of the four sets of chromosomes and will be of the genetic constitution (aaaa). A cross with a homozygous (true-breeding) full-colored individual (AAAA) will in the

second generation produce full-colored (AAAA), albinos (aaaa), and three genetically different types of intermediates (AAAa), (AAaa), and (Aaaa). Whereas, in the diploid there were only three possible genetic types, there will be five in the tetraploid.

TABLE 2

A comparison of a cross between albinism and color in a diploid and an autotetraploid.

	Diploid	Tetraploid
Color parent	AA	AAAA
Albino parent	aa	aaaa
First generation	Aa	AAaa
Second generation	AA....25%	AAAA.... 2.8%
		AAAa....22.2%
	Aa....50%	AAaa.....50.0%
		Aaaa.....22.8%
	aa.....25%	aaaa..... 2.8%

The differences between the two examples are set out diagrammatically in Table 2. It will be seen that in the tetraploid second generation as compared with the diploid, there are (1) three kinds of intermediates instead of one, (2) a much higher proportion of intermediates (94% instead of 50%). This will result in the tetraploid being tremendously more variable (using the word in its biological sense). In our hypothetical case of albinism in a population breeding at random and with, as is usually the case, the full-colored forms somewhat more variable than the albinos, we may expect in the diploid a large number of dark blues (AA), a large number of intermediates (Aa) and a few whites (aa). With exactly the same premises we will find in the tetraploids, very few dark blues and a large proportion of intermediates of various shades of blue and a very few pure albinos or none at all.

The same situation which has been outlined for albinism will apply to all the other genes; all will be present in sets of four instead of in sets of two. The change from pink flower to blue flower is apparently mainly due to a single factor. In a population of *T. bracteata* segregating for albinism and for pink we would expect to find only light and dark pink, light and dark blue, and white. In a similar population of *T. reflexa* we might expect to find blues, various intermediate magentas, and perhaps a few pinks, all in many degrees of color intensity.

These hypothetical deductions (which had been worked out from greenhouse material before we examined wild populations) are interesting because they agree exactly with what we actually *did* find. Large populations of *T. reflexa* were studied at five localities and *T. bracteata* was studied at two widely separated ones. The

data are summarized in Table 3. Those on flower color are difficult to present because of the variability of the tetraploids. In the diploid *T. bracteata* it was a simple matter to score the flowers as either pink or blue. Among the plants of *T. reflexa* any attempt at classification (aside from the extremely rare pure pinks) was extremely difficult and frankly artificial. In Table 3 an attempt is made to record the prevailing color types in each colony and the actual number of pure pinks or pure albinos. In another section of this paper one colony is taken up in as great detail as possible. The variation there reported is typical.

The number of genes segregating in a wild population is probably to be numbered by the thousands. For each of these the same situation will prevail which has been outlined in detail for those for pink and for albinism. The net result will be a tremendous increase in the total possible number of geneotypes in each population, and in the number and proportion of intermediates. Nearly every taxonomist who has worked with *T. reflexa* has commented on its peculiar variability. While the fact that it is a tetraploid (and practically an auto-tetraploid) does not explain all the peculiarities met with in this species, it is responsible for many of them.

Students of the group have commented on the fact that some species of *Tradescantia* customarily produce both pink-flowered and blue-flowered plants, while other species do not. Rose (1899) for instance, has included this characteristic in forming his specific descriptions. The cytological and genetical data reported above provide a logical explanation for this interesting difference.

TABLE 3

Variation in flower color in populations of *T. reflexa* and *T. bracteata*.

SPECIES	LOCALITY	PREVAILING FLOWER COLORS	NO. OF PURE PINKS	NO. OF PURE WHITES
T. reflexa	Algonquin, Webster Groves, Missouri	Blue, blue-magenta, magenta, magenta-pink	1	0
T. reflexa	S. Webster, Missouri	Blue, magenta-blue, magenta-pink	0	0
T. reflexa	Hamburg, Missouri	Dark-blue, blue, blue-magenta	0	0
T. reflexa	Hillsboro, Missouri	Dark-blue, blue	0	0
T. reflexa	Ullin, Illinois	Dark-blue, magenta, magenta-pink	0	0
T. reflexa	Schoolcraft, Mich.	Dark-blue, grey-blue, deep magenta, pale magenta	0	0
T. bracteata	Portage des Sioux, Mo.	Bright blue 39, blue-magenta 1	14	0
T. bracteata	Tama, Iowa	Blue 1100 ±	380 ±	6

VEGETATIVE REPRODUCTION IN TRADESCANTIA

Throughout his paper on the Tradescantiae, Darlington (1929) has assumed that *T. virginiana*[1] is propagated mainly, if not entirely, by vegetative means. He presents no experimental evidence for this conclusion other than to describe the cytological conditions which according to his theories make vegetative propagation obligatory. The following quotations are representative of his point of view: p. 254. "The fact that we have forms of *Tradescantia virginiana* with fragments that do not answer to the requirements of meiosis merely *emphasizes the unimportance of sexual reproduction in preserving this species*."

P. 254. "*T. virginiana* itself has drifted into an evolutionary back water in which *vegetative propagation has become excessively important.*

P. 278. "In *Tradescantia crassifolia* and *T. bracteata*, however, the various abnormalities must *reduce seed-production to negligible proportions if they reproduce themselves normally.*"

P. 279. "More recently Bush (1904) for example, has distinguished 18 different species from Texas alone; these would probably all resemble the types described cytologically [They do not. The seven that we have examined so far have been diploids.] and would be interfertile so far as they were fertile at all. It need hardly be said that none of them would be consistently true-breeding."

As will be demonstrated below this very logical theory is completely erroneous. We have not found the slightest scrap of evidence to support the thesis that tetraploid Tradescantias like *T. virginiana* and *T. reflexa* are dependent upon vegetative propagation. On the other hand we have found abundant evidence that it is even less highly developed among them than among the simple diploids from which they probably arose. Darlington's erroneous conclusions are probably due in part to his ignorance of the fact that these species are usually self-sterile.[2] Isolated specimens in gardens or greenhouses cannot be made to set seed. Moore (1917) had previously reported the fact, and we have been unable to obtain seed from self-pollination of any of the plants we have under cultivation, though they set seed readily in cross-pollinations.

There are two ways in which Darlington's hypothesis can be tested. We have evidence on both points.

[1] It should be remembered that Darlington includes not only the closely related species *T. reflexa*, but also the southwestern low-growing species *T. bracteata*, *T. humilis*, etc., as varieties and sub-species of "*T. virginiana* L. (U. S. A.)."

[2] On p. 272 and again on p. 274 he uses the hypothesis of "*continued self-fertilization*" to explain his results.

I. SEED PRODUCTION.

Prolonged search during the fruiting season failed to reveal a plant which was not producing seeds. No doubt such plants do exist, but none was found among the several hundred we examined. Most of the plants we examined were setting abundant seeds and many of the populations included young seedling plants.

II. VARIABILITY BETWEEN PLANTS IN WILD POPULATIONS.

The morphological consequences of vegetative and sexual reproduction are so different that a careful morphological analysis of wild populations will yield critical evidence. Such an analysis will do more than demonstrate merely the occurrence or non-occurrence of vegetative reproduction. It will make possible an evaluation of the relative importance of sexual and vegetative reproduction in maintaining the species. If vegetative reproduction is of any considerable importance its existence will be demonstrated in three different ways:

(1) The persistence of an actual organic connection between the parent plant and its vegetatively derived offspring.

(2) the frequent occurrence of morphologically indistinguishable plants which had originated vegetatively from a single individual, but in which the connection had died out or had been severed.

(3) The occasional appearance of a single, isolated individual.

These are all probably self-evident, except perhaps (3) which follows from the fact that if a species reproduces actively from seeds as well as by vegetative means, a single individual introduced into a virgin locality will soon be surrounded by seedlings, which will vary among themselves.

It would not have been surprising to have found any or all of these conditions in *Tradescantia* since all three are commonly met with among the Monocotyledons. An entire meadow is occasionally colonized by a single clone of *Iris* nor is it uncommon in that genus to find neighboring plants with no remaining evidence of an actual physical connection, between whose flowers there are no greater differences than exist on either plants. On all three of these points, however, we have evidence that vegetative reproduction is of minor importance in the tetraploid *T. reflexa*.

(1) Among the plants of *T. reflexa* which we studied there was never the slightest evidence of an organic connection between neighboring plants. Spreading by rhizomes was limited to a compact area around the parent stem.

(2) In not a single instance did we find two neighboring plants which could not be easily distinguished (see Table 4 and text fig. 2). Transplant experiments with a few of these types showed

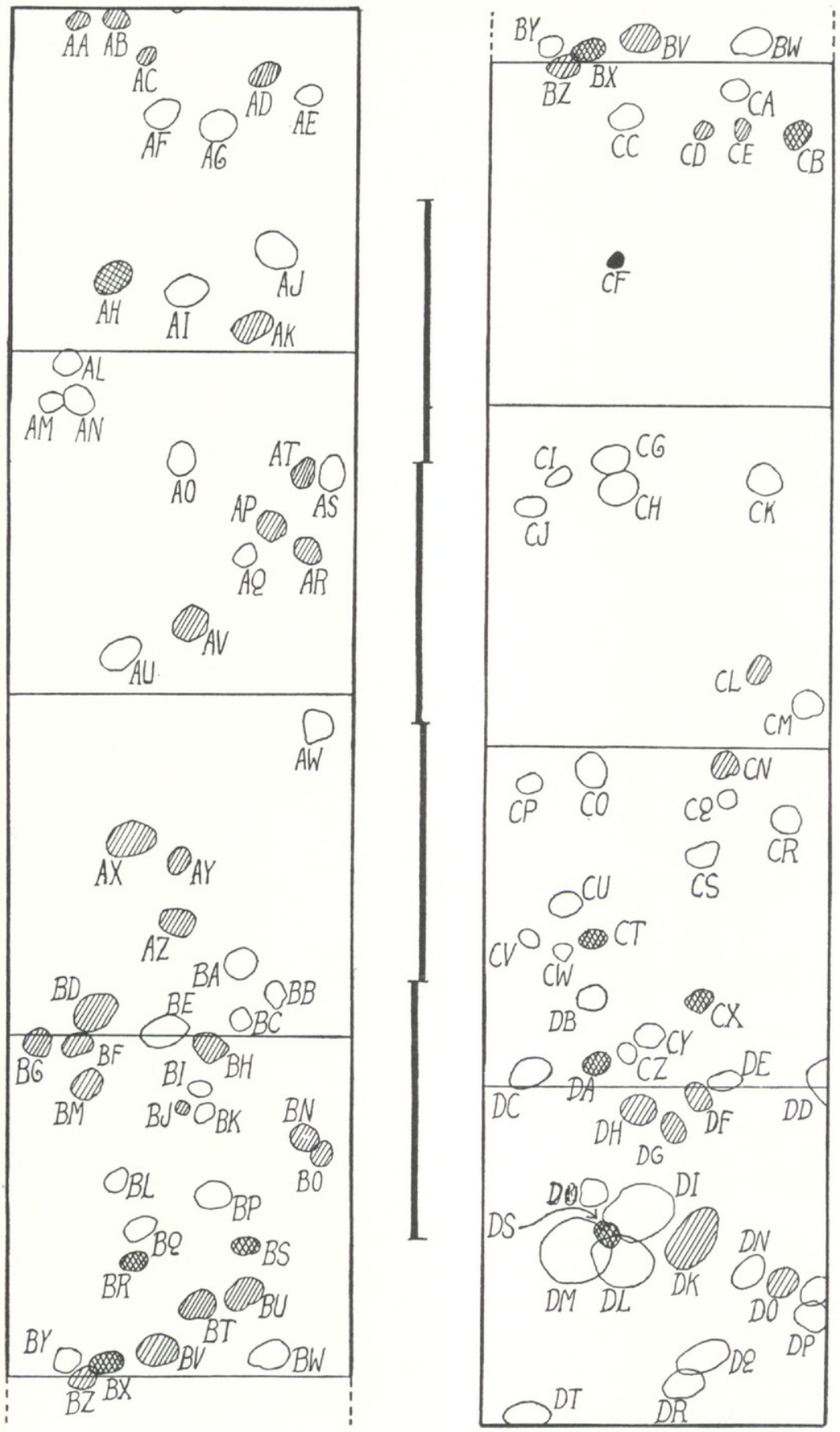

Figure 2. A belt transect of eight two-meter quadrats at Algonquin, Missouri. Each circle represents a single clone and the area is roughly that of the crown at the time of flowering. Unshaded plants bore blue flowers, diagonal lines represent blue-magenta flowers, cross-hatching magenta, and solid black represents pink. Further description of the plants in Table 4. The divisions of the scale represent five feet.

that these individual differences were largely inherent and persisted under cultivation.

(3) We never found an isolated clone of *T. reflexa*. In every case if there was one plant there were from a dozen to several thousand other plants nearby. Although a clone of *T. reflexa* will persist for years under cultivation, gradually increasing in size, the largest we found in nature had a crown under three feet in diameter, and the crowns of the majority of wild plants are less than six inches across. As a matter of fact, the diploid species *T. bracteata* is more vegetatively vigorous than its tetraploid relative and often produces clones over two feet in diameter.

A DETAILED STUDY OF ONE COLONY OF T. REFLEXA

A typical colony of *T. reflexa* was chosen for intensive study and a part of the data collected are presented in Table 4 and figure 2. The colony occupied two or three acres along the Missouri Pacific right of way near the Algonquin suburban station in Webster Groves, Missouri. Eight two-meter quadrats were laid out in one belt transect. The individual clones were scored for height, pubescence of sepals and ovary, flower color, and number of stems.

While the variation in flower color and in pubescence was somewhat greater than we usually found, it was by no means exceptional. The variation in height of stem and size of clone was, on the other hand, less extreme than the average. The seed capsules of Tradescantia explode when ripe and discharge their seeds over a radius of a few feet. If a colony is left undisturbed there would soon be a tendency for seedlings to show greater resemblances to neighboring plants than to the colony as a whole. There is some circumstantial evidence from this colony and from other colonies that in this way seedlings tend to grow up around a prolific mother plant and form small "neighborhoods" in which adjacent plants resemble one another more closely than they do the colony at large. It will be seen from figure 2 that plants of different colors are not distributed at random. This was even more evident when the whole colony was examined. Although no two neighboring plants were identical there was often a "family resemblance" between them, and pink and magenta flowered plants tended to occur in groups.

A SURVEY OF SOUTHWESTERN TRADESCANTIAS

In addition to the material which we collected personally we were enabled through the kindness of Dr. B. C. Tharp of the University of Texas and Dr. D. W. Moore of the University of Arkansas to make a preliminary survey of the Tradescantias from those regions.

TABLE 4

Clone	Height of Stem	Pubescence on Sepals	Pubescence on Ovary	Flower color (approximate)	No. of stems
AA	short	tufted at apex	glabrous	medium magenta	
AB	short	scattered	glabrous	medium magenta	
AC	short	scattered	a few hairs at base of style	medium magenta	
AD	medium	tuft at apex	glabrous	medium magenta	Unless Otherwise Indicated there was One Stem per Clone
AE	medium	scattered	hairs at base of style	medium blue	
AF	short	scattered	glabrous	blue	
AG	medium	scattered	glabrous	blue	
AH	medium	scattered	hairs at base of style	magenta	
AI	medium	tuft at apex	glabrous	blue	
AJ	medium	lightly scattered	glabrous	blue	
AK	medium	lightly scattered	glabrous	medium magenta	
AL	medium	lightly scattered	glabrous	dark blue	
AM	medium	lightly scattered	glabrous	dark blue	
AN	medium	lightly scattered	glabrous	dark blue	
AO	medium	lightly scattered	glabrous	dark blue	
AP	medium	lightly scattered	glabrous	medium magenta	
AQ	medium	lightly scattered	glabrous	blue	
AR	medium	lightly scattered	glabrous	medium magenta	
AS	short	lightly scattered	glabrous	blue	
AT	medium	lightly scattered	glabrous	medium magenta	
AU	tall	tuft at apex	glabrous	blue	
AV	medium	tuft at apex	glabrous	medium magenta	
AW	medium	tuft at apex	glabrous	blue	
AX	medium	tuft at apex	glabrous	medium magenta	
AY	short	scattered	glabrous	medium magenta	
AZ	tall	scattered	glabrous	medium magenta	three stems
BA	tall	tuft at apex	glabrous	blue	
BB	medium	tuft at apex	glabrous	blue	
BC	short	scattered	glabrous	blue	
BD	short	scattered	glabrous	medium magenta	
BE	past blooming				
BF	medium	scattered	glabrous	medium magenta	
BG	medium	tuft at apex	glabrous	medium magenta	
BH	tall	tuft at apex	glabrous	medium magenta	
BI	medium	lightly scattered	hairs at base of style	light blue	
BJ	medium	tuft at apex	hairs at base of style	medium magenta	
BK	medium	tuft at apex	glabrous	medium blue	
BL	short	scattered	glabrous	blue	
BM	medium	scattered	glabrous	medium magenta	
BN	medium	scattered	glabrous	medium magenta	
BO	medium	scattered	glabrous	medium magenta	
BP	medium	scattered	glabrous	blue	
BQ	medium	scattered	glabrous	blue	
BR	medium	tuft at apex	glabrous	magenta	
BS	medium	tuft at apex	glabrous	magenta	
BT	medium	tuft at apex	glabrous	medium magenta	
BU	short	scattered	glabrous	medium magenta	
BV	medium	scattered	glabrous	medium magenta	two stems
BW	medium	scattered	glabrous	blue	
BX	medium	tuft at apex	glabrous	magenta	two stems
BY	medium		through blooming		
BZ	tall	scattered	glabrous	blue magenta	
CA			Seedling		
CB	tall	scattered	glabrous	madium magenta	

TABLE 4—Continued

Clone	Height of Stem	Pubescence on Sepals	Pubescence on Ovary	Flower color (approximate)	No. of stems
CC	tall	scattered	glabrous	dark blue	four stems
CD	medium	scattered	glabrous	dark blue magenta	
CE	medium	tuft at apex	glabrous	medium magenta	
CF	short	tuft at apex	hairs at base of style	pink	
CG	medium	tuft at apex	glabrous	blue	
CH	medium	scattered	glabrous	dark blue	
CI	tall	tuft at apex	glabrous	dark blue	two stems
CJ	tall	tuft at apex	glabrous	dark blue	two stems
CK	medium	scattered	glabrous	light blue	
CL	tall	tuft at apex	glabrous	dark blue magenta	three stems
CM	short	tuft at apex	glabrous	blue	
CN	short	tuft at apex	glabrous	dark blue magenta	two stems
CO	tall	tuft at apex	glabrous	dark blue	
CP	medium	scattered	glabrous	dark blue	
CQ	tall	scattered	glabrous	dark blue	three stems
CR	medium	tuft at apex	glabrous	dark blue	seven stems
CS	medium	scattered	glabrous	blue	four stems
CT	short	scattered	glabrous	magenta	
CU		Seedling			
CV	short	scattered	glabrous	blue	
CW	medium	tuft at apex	glabrous	blue	
CX	short	tuft at apex	glabrous	magenta	
CY	medium	scattered	glabrous	blue	seven stems
CZ	medium	scattered	glabrous	blue	
DA	medium	scattered	glabrous	dark magenta	
DB	short	tuft at apex	glabrous	light blue	
DC	tall	tuft at apex	glabrous	blue	
DD	tall	tuft at apex	glabrous	medium blue	large clone
DE	medium	scattered	glabrous	blue	
DF	short	scattered	glabrous	blue magenta	
DG	short	tuft at apex	glabrous	blue magenta	
DH	short	tuft at apex	glabrous	blue magenta	
DI	tall	scattered	glabrous	light blue	large clone
DJ					
DK	medium	scattered	glabrous	blue magenta	
DL	medium	scattered	glabrous	dark blue	large clone
DM	tall	tuft at apex	glabrous	light blue	large clone
DN	tall	tuft at apex	glabrous	dark blue	five stems
DO	medium	scattered	glabrous	magenta blue	four stems
DP	tall	scattered	glabrous	blue	large clone
DQ	medium	tuft at apex	glabrous	blue	
DR	medium	scattered	glabrous	blue	
DS	medium	scattered	glabrous	magenta	
DT	tall	scattered	glabrous	medium blue	seven stems
DU	medium	scattered	glabrous	light blue	

The material was forwarded just before it came into bud and was grown in the greenhouse, where material for smears was obtained. The following species were examined: (with the exception of *T. texana* the determinations are those made by Dr. Tharp.)

	P M C	Pollen Mitosis
T. humilis		
plant A	n = 6	—
plant B	n = 6 + f	n = 6 + f
T. edwardsiana[1]	—	n = 6

[1] *Tradescantia edwardsiana* Tharp in Rhodora, XXXIV. 57, fig. 1 (1932).

	P M C	Pollen Mitosis
T. hirsuticaulis	—	n = 6
T. texana	n = 6	n = 6
T. gigantea		
plant X	n = 6 + f	n = 6 + f
plant Y	n = 6	n = 6
T. occidentalis	—	n = 6
T. sp. (reflexa ?) from Texas	—	n = 6
T. sp. (reflexa ?) from Arkansas	—	n = 6

It will be noticed that whereas two of the species in the St. Louis region were tetraploids, all of the material from the southwest was diploid. One of the species from Texas and all of the plants from Arkansas were very similar to *T. reflexa* as it occurs in Missouri; just how similar could not be determined since the southern material was forced into bloom under abnormal conditions. If these plants do not belong to *T. reflexa*, they must certainly form a very closely related species. Since the Missouri and other northern material of *T. reflexa* was all tetraploid it is therefore quite possible that polyploidy is intraspecific in *Tradescantia* and that diploid and tetraploid races may occur within the same species.

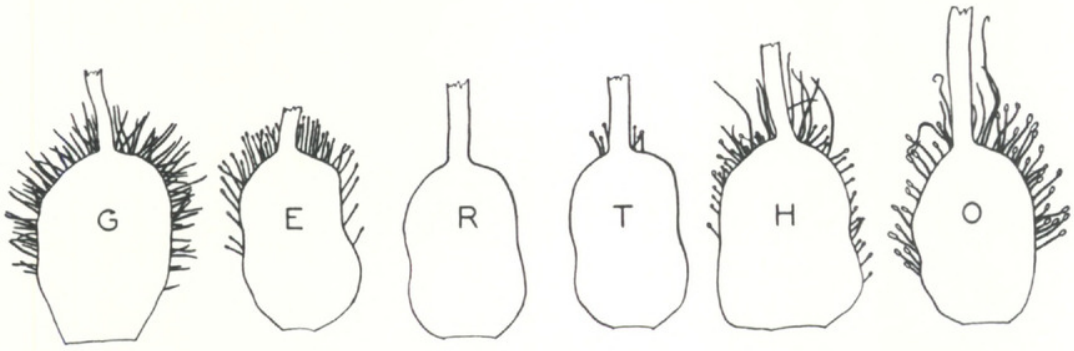

Figure 3. Ovaries of six species of *Tradescantia* from the neighborhood of Austin, Texas. Drawn, greatly enlarged, with camera lucida. From left to right: G; *T. gigantea;* E; *T. edwardsiana;* R; *T. reflexa;* T, *T. texana;* H, *T. hirsuticaulis;* O, *T. occidentalis.*

It is particularly interesting that the tetraploid Tradescantias should be more northerly than the diploids. Sax (1931) has reported in the closely related genus *Rhoeo*, the artificial production of tetraploids by exposure to low temperatures. A similar geographical position for tetraploid races and species to the north of their diploid relatives has been reported for a number of genera. Hagerup (1928) collected six such cases in the Bicornes alone and has recently summarized the evidence on polyploid geographical races (1932). It is particularly interesting that Mangelsdorf and Reeves (1931) working with another American monocot of tropical affiliations (*Tripsacum dactyloides*) have found that the plants collected in Texas are diploids while those from the north and east are tetraploids.

It may be well in passing to point out that the differences between the seven diploid species from Texas are quite as great, on the whole, as are those between the three Missouri species. Polyploidy here, as elsewhere, has introduced complexity into inter-specific relationships, but species differentiation has taken place to an even greater extent in regions where polyploidy was absent.

Table 5 summarizes the outstanding differences between these species. Camera lucida outlines of their ovaries are shown in figure 3. While instances of inter-specific hybridization are not unknown, most of these Texas species are kept apart by habitat differences and maintain themselves as recognizable units over a wide area.

TABLE 5—A TABULAR COMPARISON OF SPECIES DIFFERENCES IN TEXAS AND MISSOURI

Species	Stem	Floral leaves	Pubescence on		
			Leaves	Sepals	Ovary
Texas species:					
T. texana	short, weak branched	long, equal	long, villous	dense, glandular	a few glandular hairs at top
T. gigantea	tall	short, subequal, densely pilose	glabrous	dense, non-glandular	very dense, non-glandular
T. hirsuticaulis	tall	short, unequal	hirsute	sub-glandular	glandular and non-glandular
T. humilis	short	unequal	hirsute	glandular	dense, glandular
T. occidentalis	slender	slender	glabrous	scattered glandular	glandular and non-glandular
T. sp. (reflexa ?)	medium	long, unequal	glabrous	glabrous except for tuft at apex	glabrous
Missouri species:					
T. reflexa	medium to tall	long, unequal	glabrous	glabrous except for tuft	glabrous
T. bracteata	short	very long, subequal	scattered, glandular	glandular	dense, glandular
T. pilosa	tall zig-zag	sub-equal	scattered, pilose	glandular pilose	scattered, glandular

CONCLUSIONS

It should be remembered that the following conclusions are little more than working hypotheses and that they are put forward tentatively at the end of our first year of intensive work. In beginning this study we had as our objectives (I) the description of the species of *Tradescantia* as they occur in nature and (II) the evaluation of the evolutionary processes which are taking place in them at the present time.

I. As regards the description of these species and their separation and classification we feel that they are a difficult group but by no means an impossible one. Their inter-specific relationships are not nearly so intricate as are those of such genera as *Rubus* and *Crataegus*, for instance. In this connection we have found the pubescence on the ovary a particularly useful character because it varies so little within species. A colony of Tradescantias may vary strikingly in size and general aspect from plant to plant and yet the pubescence on the ovary will be the same throughout the colony. The pubescence also varies widely from species to species. It may be dense, or sparse, or restricted to one part of the ovary, or completely wanting. The hairs may be long or short, and glandular or non-glandular. Used in connection with other characters it is very helpful in working out specific relationships.

II. In evaluating the evolutionary processes which are taking place at the present time, we have evidence on three, fragmentation, polyploidy and hybridization.

FRAGMENTATION.

In every species in which we were able to examine a number of different plants, we found individuals with supernumerary fragment chromosomes. That is, in addition to the normal chromosome complement for the species, these individuals had one or two fragment chromosomes, much smaller than the rest (Plate 45, figs. A, K). In at least two cases these fragments paired regularly at the reduction division and were distributed to all the germ cells. We found fragments occurring with roughly the same frequency in all the species which we investigated. If, as seems probable, they affect the external morphology of those plants which bear them, we have here a unique case in which one of the causes of variation within species is not itself effective in forming new species. Had it been so we should have found entire species or races which were characterized by the possession of supernumerary chromosomes.

POLYPLOIDY.

In these species of *Tradescantia* polyploidy is apparently intraspecific, with consequent division of those species possessing it into diploid and tetraploid races. It apparently allows a northern extension of the range in those species in which it has occurred. It increases manyfold the variation between individual plants. Its "blurring" effect upon variation in flower color can actually be demonstrated and a similar effect upon morphological characters is inferred from the peculiar variability of the tetraploid species, *T. reflexa* and *T. virginiana*. In the section of the genus which we have

studied, polyploidy does not occur at the center of specific diversity but is instead characteristic of the northern periphery of the genus. It must therefore be of relatively minor importance as a factor in originating new species though it multiplies the complexity of *inter*-specific and *intra*-specific relationships.

HYBRIDIZATION.

Although this undoubtedly occurs we have as yet found little actual evidence for it. The colony from Hillsboro, described above, may perhaps have resulted from previous hybridization between *T. reflexa* and *T. bracteata*. An apparent example of hybridization between *T. humilis* and *T. reflexa* has just been discovered in the vicinity of Austin, Texas.

SUMMARY

Three species of *Tradescantia* are common in the region about St. Louis, Missouri, two tetraploid species *T. reflexa* and *T. pilosa*, and one diploid species, *T. bracteata*. White-flowered and pink-flowered forms are frequent in *T. bracteata* while in the two tetraploid species they are rare. Furthermore various intermediate magenta shades are common in the tetraploid *T. reflexa* but are not found in *T. bracteata*. This is shown to follow logically from the fact that *T. reflexa* is practically an auto-tetraploid.

Darlington's assumption of highly developed vegetative reproduction in tetraploid Tradescantias is found to be without any foundation in fact.

The inter-clonal variation of a single colony is presented in detail.

Seven species of *Tradescantia* from eastern Texas were found to be diploids.

The evolutionary importance of fragmentation, polyploidy, and hybridization is briefly discussed.

ACKNOWLEDGMENT

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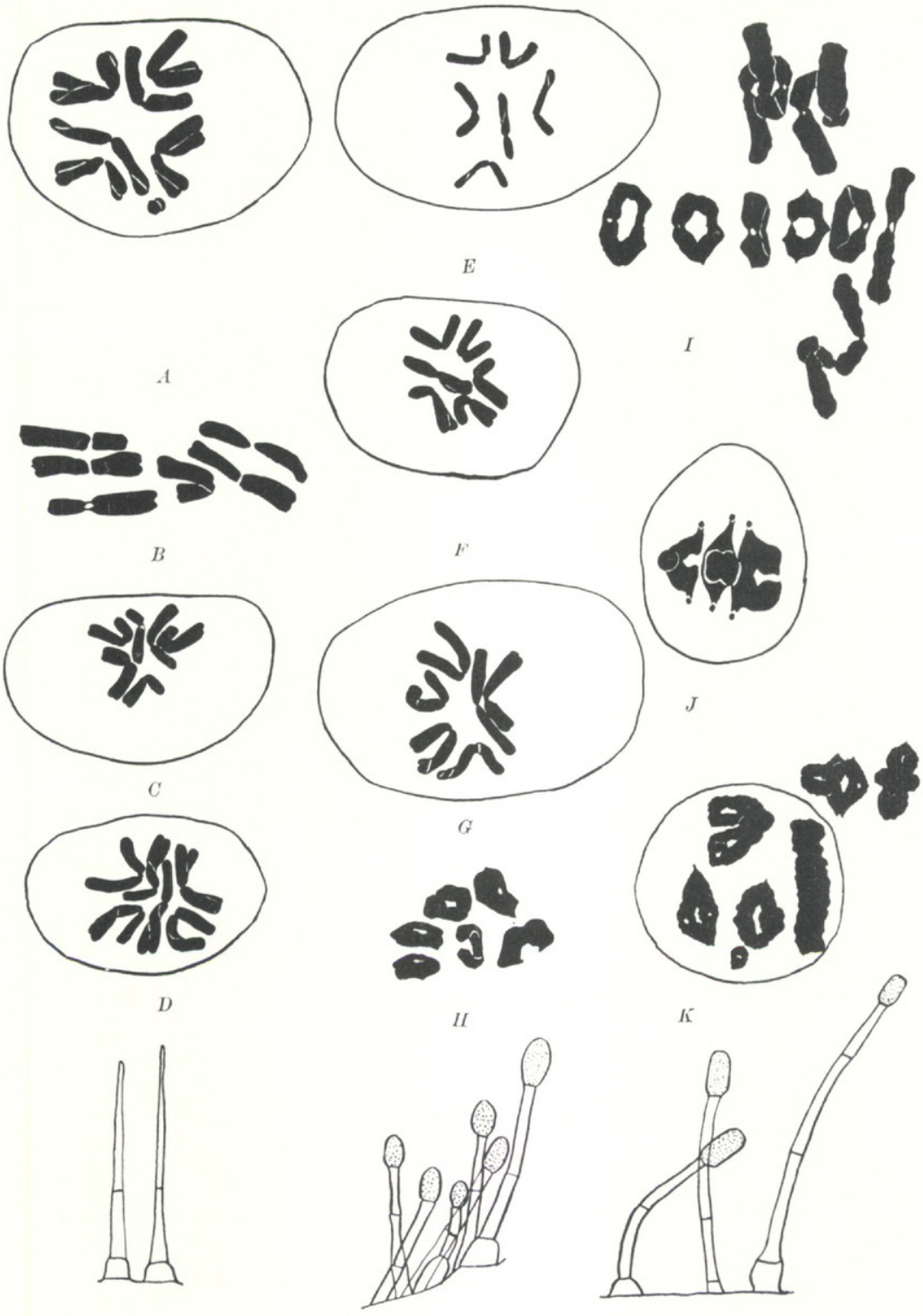

CHROMOSOMES AND OVARY HAIRS OF TRADESCANTIA SPECIES

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EXPLANATION OF PLATE 45

Chromosomes of Tradescantia species. All drawn with camera lucida at bench level from temporary or permanent smears. I drawn from a plant from eastern Missouri. The others are all from plants collected in the neighborhood of Austin, Texas. In figures I and K the different levels have been drawn separately to avoid confusion.

A. *T. gigantea*. Pollen mitosis. n = 6 × f.
B. *T. texana*. Pollen mitosis. Smear slightly crushed. n = 6.
C. *T. humilis*. Pollen mitosis. n = 6.
D. *T. edwardsiana*. Pollen mitosis. n = 6.
E. *T. occidentalis*. Pollen mitosis. n = 6.
F. *T. sp.* (*reflexa* ?). Pollen mitosis. n = 6.
G. *T. hirsuticaulis*. Pollen mitosis. n = 6.
H. *T. humilis*. P M C. 6 bivalents.
I. *T. reflexa*. P M C. 6 bivalents and 3 quadrivalents.
J. *T. humilis*. P M C. Metaphase showing "insertion points."
K. *T. gigantea*. P M C. 6 bivalents and one pair of fragment chromosomes. Two of the bivalents have been drawn at one side for clearness.

Below. Ovary hairs, drawn greatly enlarged with camera lucida. Left, *T. gigantea* from Austin, Texas; center, *T. bracteata* from Portage des Sioux, Missouri; right, *T. pilosa* from Hermann, Missouri.

A COMPARATIVE STUDY OF THREE PHYTOPHTHORA DISEASES OF LILAC AND OF THEIR PATHOGENS

KENNETH S. CHESTER

With a diagram and plates 46 and 47

I. INTRODUCTION

A SERIOUS DISEASE of Lilacs caused by *Phytophthora Syringae* Kleb. has been recognized for many years in European lilac plantings. Very recently a second lilac disease attributed to *Phytophthora cactorum* (L. & C.) Schroet. has been found in America. A third lilac disease due to a distinct form of *Phytophthora* has been under observation at the Arnold Arboretum for several years. The present paper beside first reporting and describing the disease last named and its causal organism also reports a comparative study of the three Phytophthora diseases of Lilac with respect to the symptoms, etiology, and control of the diseases in question.

II. HISTORICAL

The first report of a Phytophthora disease of Lilac was that of Berkeley in 1881 (4) in which was described under the name *Ovularia Syringae* Berk. a fungus comparable to *Phytophthora infestans* (Mont.) de Bary which caused large brown patches on lilac leaves. Berkeley observed the production of conidia through the stomata and suggested that the conidia might germinate by means of zoospores. The following year Smith (31) first saw the oospores of Berkeley's fungus and described them. The germination of the conidia of Berkeley's fungus by means of zoospores was observed by A. S. Wilson in 1886 (33). Nine years later in 1905 (16) Klebahn published a short account of a disease of Lilac caused by what was in all probability the same fungus as that of Berkeley. The identity of Klebahn's fungus and that of Berkeley was not recognized, however, and Klebahn's disease was attributed to a new species and genus of fungus, *Phloeophthora Syringae* Kleb. According to Klebahn's observations the disease was seated in the cortex of mature lilac branches, was manifested by a browning and death of the cortex, and was apparently not related to any leaf disease. Klebahn succeeded in obtaining pure cultures of the fungus and in producing typical lesions on artificially inoculated plants. Although the sexual structures were seen, there was no apparent production of conidia, which latter fact, together with the location of the disease in the cortex of woody stems, led to the assumption of a new genus.

The following year Klebahn continued his studies (17) and brought out the relation of the disease to the abnormal environmental conditions of the lilac forcing industry. A much more extended account of the same disease is contained in a later work by the same author in 1909 (18), reviewed by Hasselbring in 1910 (13), in which he finally observed the conidia and recognized the true nature of the fungus. The name was accordingly changed to *Phytophthora Syringae* (Kleb.) Kleb. In this longer account Klebahn reported detailed investigations of the symptoms produced on stored and forced Lilacs, the morphology and biology of the fungus, the proof of the parasitism of *Phytophthora Syringae*, and the control measures which had been found to be effective in reducing the disease. In addition to infection experiments with Lilacs, the author also found the fungus to be capable of parasitism of a variety of other host plants. Klebahn's observations showed the disease to be present in 1909 in Hamburg and Cuxhaven, whence he believed it had been introduced from France. Later in 1909 Lustner (24) also reported it from Hohenheim and Frankfurt am Main. In 1910 Himmelbaur (15) repeated Klebahn's studies of *Phytophthora Syringae* and confirmed the latter in finding *P. Syringae* distinct from any previously reported species of *Phytophthora*.

By 1913 the fungus had spread to Holland according to the report of Schoevers (29) and was there likewise found to be causing a serious disease of cultivated lilac plants. The following year G. W. Wilson studied *P. Syringae* from the taxonomic standpoint (34), and beside confirming the earlier descriptions of the fungus the author was the first to point out the probable identity of Klebahn's fungus with that of Berkeley's. The name *Phytophthora Syringae* (Kleb.) Kleb., however, is retained. In 1918 Arnaud (1, 2) reported the appearance of the disease in France, where it was causing minor injury in a hedge of Lilac. Here for the first time the conidiophores of *Phytophthora Syringae* were observed occurring in nature on infected Lilacs.

Up to 1922 the disease had been reported from England, Germany France, and Holland. In that year Lafferty and Pethybridge (19) reported an isolation of *Phytophthora Syringae* from rotted apple fruit in Ireland. Specimens of lilac leaves probably injured by *P. Syringae* had also been received by the same authors. In the paper in question the authors reviewed the morphology of the sexual organs of *P. Syringae* and reported for the first time the presence of both amphigynous and paragynous antheridia within the species.

Phytophthora Syringae was shown to be capable of saprophytic life in the soil by de Bruyn in 1922 (5). Two years later Miss de

Bruyn published a continuation of her studies (6, 7) in which were reported an extensive series of infection experiments on Lilac. In the latter papers she found that the disease occurred in greatest destructiveness in those seasons in which there was abnormal rainfall in August or September. Infection was found to take place in the winter months, from December till April in the cortex, and from October till February in the buds. Hand picking of the leaves as a control measure was suggested, but in a later paper (8) the author found that hand picking of the leaves was so injurious to the blossoms as to eliminate it as a control measure.

The only record of *Phytophthora Syringae* in America is that of Hedges in 1929 (14). Miss Hedges found a fungus believed to be *P. Syringae* fruiting on several blighted young lilac shoots in Washington. The lesions had the appearance of those due to fire blight (*Bacterium Syringae*), and the attack was severe. Since the lesions described were on young shoots examined in May, it is possible that the *Phytophthora* found was one of the other two species here considered, since *P. Syringae* normally does not primarily attach the succulent tissues of lilac.

Phytophthora cactorum (L. & C.) Schroet., originally described as *Peronospora cactorum* by Lebert and Cohn in 1870 (20) and since investigated by many workers, is known to parasitize a great variety of host plants. On Lilac, however, it has been recognized only recently. In 1929 R. P. White described a disease of *Rhododendron* and Lilac from New Jersey, with which was associated this species of *Phytophthora* (35). Cross infection experiments proved that the same fungus was responsible for the disease in both hosts. On Lilac the disease takes the form of a dying-back of suckers and of leaf infections. Production of conidia was observed on the Lilac. As control measures for Lilacs, White suggested generous spacing of the plants, removal of dead wood, and use of a dormant spray of lime-sulphur together with summer applications of Bordeaux mixture.

With regard to the third type of *Phytophthora* causing disease in Lilac, no record has heretofore appeared in the literature.

In addition to the primarily pathological literature dealing with the lilac Phytophthoras, a number of purely mycological papers have dealt with *P. Syringae* and *P. cactorum*. An attempt will not be made to go into the taxonomy of these species at the present, but it may merely be said in passing that the two species are considered perfectly distinct by all of the leading students of the genus (G. W. Wilson, 1914, 34; Rosenbaum, 1917, 26; Leonian, 1925, 21; Tucker, 1931, 32).

III. MATERIALS AND METHODS

The cultures of *Phytophthora* employed in the present study were obtained from the following sources: (a) a culture of *Phytophthora Syringae* isolated by Miss de Bruyn from Lilac in Holland and obtained from the Centraalbureau voor Schimmelcultures at Baarn in 1928; (b) a culture of *Phytophthora cactorum* isolated from Lilac in New Jersey by R. P. White and sent to me by Dr. White in 1929; (c) several cultures of the same organism isolated from Lilac by the writer in 1929; (d) a third distinct strain isolated from Lilac in the Arnold Arboretum by the writer in 1929 and hereafter referred to as *Phytophthora* "Type A."

Stock cultures of the various strains were maintained on potato-dextrose agar. For the production of the spore forms special techniques were necessary. None of the strains produced sporangia in appreciable amount on potato-dextrose agar. For sporangium production the technique originally devised by Klebs was employed. Tiny fragments of mycelium of active cultures were transferred to large test-tubes each containing about 20 cc. of pea decoction. After several days growth in the pea broth at room temperature the mycelial mats were transferred to sterile pond water, the sterile water being renewed frequently. Distilled water did not prove satisfactory for this purpose. Abundant production of sporangia resulted at room temperature within 24 to 48 hours after transferral to sterile water. The production of sporangia was also induced by the conventional employment of Petri's mineral solution

(.4 gm. $Ca(NO_3)_2$ + .15 gm. KH_2PO_4 + .15 gm. $MgSO_4$
+ .06 gm. KCl + 1000 cc. H_2O),

although Petri's technique proved much less satisfactory than that of Klebs for the species of *Phytophthora* involved.

Oospore formation was brought about by the employment of special solid media, the requirements differing for the different strains of *Phytophthora* under consideration. *Phytophthora cactorum* readily reproduced sexually on a wide variety of solid substrata. Among these steamed corn-meal, steamed green bean pods, steamed carrot, lima bean agar, oatmeal agar, and corn-meal agar proved very favorable. *Phytophthora Syringae* produced oospores with apparent difficulty, sterile lilac leaf extract (10), steamed carrot, steamed corn-meal, and oatmeal agar in the order named yielding the most satisfactory results. *Phytophthora* "Type A" produced oospores abundantly on steamed green bean pods, lima bean agar, and corn-meal agar.

Since the morphology and the physiology of the genus *Phytoph-*

IV. COMPARATIVE STUDY OF THE SPECIES OF PHYTOPHTHORA PARASITIZING LILAC

As a preliminary to a correct diagnosis of the Phytophthora diseases of Lilac and to a correct determination of the rôle played by the fungi involved in causing disease, a study of the comparative mycology of the fungi was essential. Such a study has been in progress and the experimental results and interpretations will be the subject for consideration in the present section. For convenience the experimental findings are grouped under the headings of physiology, morphology, and systematics.

A. PHYSIOLOGY

The genus *Phytophthora* has long offered to systematists a difficult problem. The morphological characters by which species of fungi are separated must necessarily be relatively invariable within the species in order that the specific differences may be determined with accuracy. Where clear cut morphological differences are lacking, as in the bacterial genera, the systematist is forced to turn to the more striking physiological characters as bases for specific distinction. The taxonomic studies of *Phytophthora*, first based upon what were believed to be sharp morphological criteria, have undergone a gradual evolution from purely morphological systems to those almost purely physiological. The reason for such an evolution in approach has been that many of the morphological characters formerly assumed to be constant within a species have since proved to be capable of wide variation according to the physiological environment. Thus the position of the antheridium relative to the oogonium was at one time felt to be a constant character in *Phytophthora* species. The work of Lafferty and Pethybridge (19) however has shown that in many species of *Phytophthora* both amphigynous and paragynous antheridia occur, although there is a tendency in a given species to form the great majority of the antheridia in one or the other manner. The size of the reproductive organs, again a character which is usually dependable in the fungi, is susceptible to such wide variation in *Phytophthora* that the only findings yielding results at all satisfactory are those based on extensive biometric studies. Other characters of the species such as method of conidial germination, method of zoospore germination, mycelial characters, and sexuality likewise exhibit high degrees of variability within a given species. Accordingly any mycological study such as the present one must necessarily be concerned both with physiological and morphological characters. Among the physiological criteria which may effectively be applied to *Phytophthora* are the rate and