SOME ASPECTS OF THE ECOLOGICAL LIFE HISTORIES OF *IMPATIENS BIFLORA* WALT. AND *IMPATIENS PALLIDA* NUTT.

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INTRODUCTION

The purpose of an ecological life history study is to enable the ecologist to explain the distribution and population density of an organism. The type of study that is described here is not the conventional morphological life history; the emphasis is not on morphological development alone, but rather on the complete and changing biology of the plant throughout the various stages in its morphological development. The focus of attention is the developing organism; the background is the changing influence of the natural environment on each developmental stage.

It is believed by the writer that an ecological life history study of a plant can be related to a biotic potential study of an animal. The biotic potential is defined by Chapman (1939) as the "...inherent property of an organism to reproduce and survive; i.e., to increase in numbers." This potential property of the organism is opposed by the factors in the environment which offer resistance to an increase in population. This resistance is termed by Chapman the "environmental resistance." Ideally, the ecologist should be able, for a particular situation, to assign exact values to the biotic potential and to the factors of the environmental resistance. The present study has progressed only far enough to provide an indication, by descriptions, of what these environmental factors may be; the coverage has been of a survey nature representing a broad exploration of methods. The size of samples used and number of tests conducted are admittedly inadequate for statistical significance; the results may be considered as suggestive only.

The basic concrete unit of research in autecology is the local population of a species rather than the individual plant or the species as a whole. The equivalent basic unit in synecology is the local sample or "stand" of a particular community. Both types of investigation require natural areas as the environment of study. Without that natural setting, the results can have little biological validity, because it is within those environmental bounds that variation and natural selection have progressed, bringing the organism to its present state of evolutionary development. Only under the natural ranges and periodicities of environmental influences can they be presumed to respond in a "normal" way; only there, can the usefulness of the adaptations developed through natural selection be viewed against the background of agents that have brought them into being; only there, the causes of local restriction to certain habitats revealed.

The local studies such as the present one are the basic building blocks of ecology. By detailed ecological life history studies of all the biotypes of a particular community, the true interrelations of that community can be revealed. A large number of these studies, properly spaced geographically will provide a sound understanding of the biological complexity of the "species" and accurate orientation of the biological relationship of closely related species.

Though, as has been pointed out, the natural area is the ideal environment for an investigation such as the one described here, some aspects of the study have been carried out in the laboratory and greenhouse, because of the many practical difficulties that arise in the use of apparatus in the field.

Impatiens biflora and Impatiens pallida were chosen for this study because of their abundance in the floodplain and bog communities both of which were easily accessible to the writer. The plants are often present in great numbers in the damp, sandy loam or peaty soil of the two types of subclimax forest; the floodplain forest and the bog forest. They frequently constitute important ground cover plants. They occur also in many wet places such as roadside ditches, moist cliffs, springs, and sometimes on gravelly stream bars and river banks.

Table I shows several characters that are helpful in distinguishing the two species. Several other differences

Table I. Characters useful in distinguishing the two species of *Impatiens*.

Character	I. biflora	I. pallida
Form of mature plant (Fig. 3)	longer branches distributed on lower half of stem; plant has ovate silhouette	longer branches distributed on upper half of stem; plant has obovate silhouette
Waxy bloom	absent	present
Leaf serrations	7-11, serrate-dentate	15-23, serrate-crenate
Anthocyanin on petiole and midribs	absent (usually)	present (usually)
Flower color	orange	pale yellow
Flower spur	long, half as long as sac	short, less than half as long as sac
Seed coat (Fig. 9)	smooth, 4 prominent longitudinal ridges, pigmentation even	rough, no definite ridges, pigmentation somewhat irregular

were found but were considered too indefinite or variable to be consistently useful. Some of these characters are: (1) the larger size of I. *pallida*, (2) the bluish-green color of I. *pallida* leaves as compared with the yellowish-green of I. *biflora*, (3) the larger cotyledon size of I. *pallida*.

The studies reported here were carried out in two major natural areas. One area was located near the mouth of Ninemile Creek, a small tributary of the Minnesota River, entering nine miles upstream from its confluence with the Mississippi. The other area was located in the bog east of Bear Paw Point in Itasca State Park. Some studies were carried out also on the floodplain at Fort Snelling, adjacent to the Mississippi River, and at Cedar Creek Forest, 33 miles north of Minneapolis.

I. ADULT PLANT

The genus *Impatiens* in Minnesota is represented by two species: *Impatiens pallida* Nutt. and *Impatiens biflora* Walt. These are the two most widespread species native to the United States. Numerous forms based on flower color differences in these two species have been described from widely scattered areas. Several of these forms have been considered separate species by some authors (Blankinship, 1905; Rydberg, 1910). A spurless species, *I. ecalcarata* Blankinship, from western Montana, Washington, and south-eastern British Columbia, and *I. occidentalis* Ryd., another western species, have also been described, but they have never been found in Minnesota. The investigation described here was confined to the two distinct species: *I. pallida* and *I. biflora*.

The two species are distributed throughout the north and northeastern part of the United States. Figure 1 is a map of North America showing distribution of the species based on descriptions by Rydberg (1910), Robinson and Fernald (1908), and Kennedy (1930). *I. biflora* has the more general distribution of the two. It extends farther north and farther south than *I. pallida*. A study of distribution by counties in Minnesota was made using material from the Herbarium of the University of Minnesota and from information on the flora of the Minnesota state parks

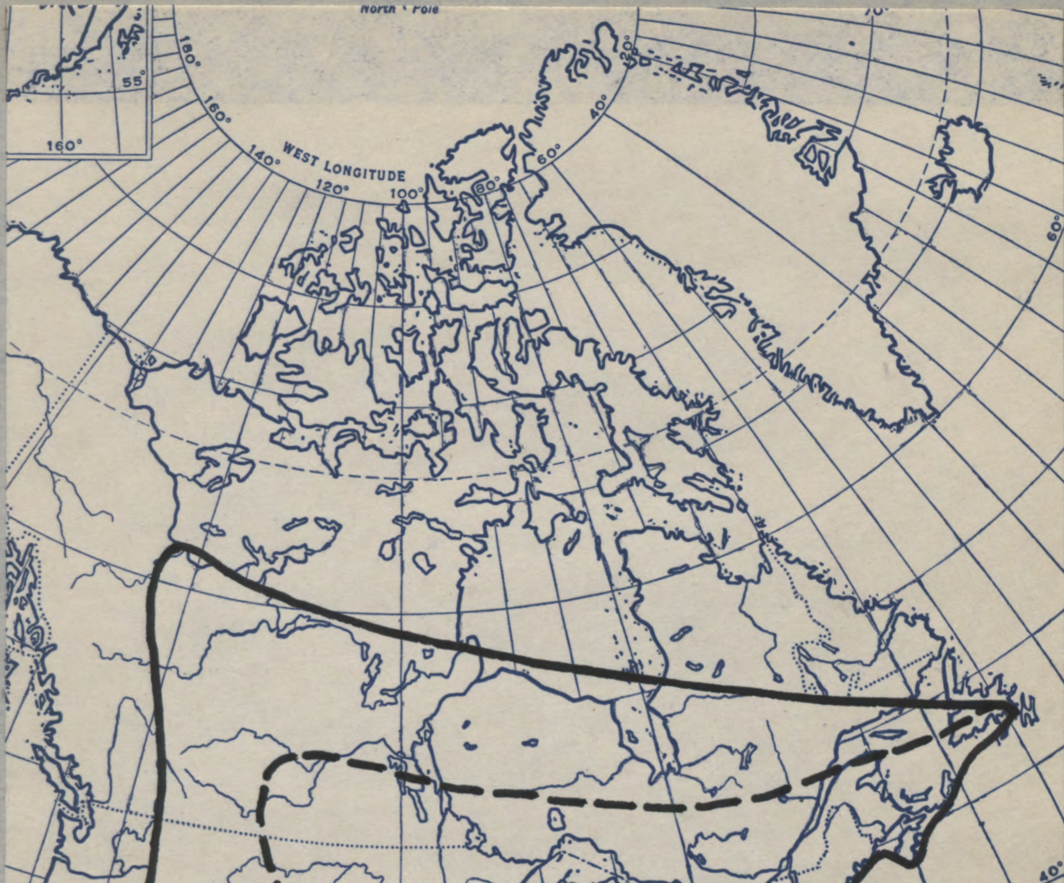


Figure 1. Part of North America showing distribution of Impatiens. The solid line indicates I. biflora; the broken line indicates I. pallida. (Base map by Rand McNally)

kindly supplied by Professor N. L. Huff and Dr. J. W. Moore. Figure 2 shows the distribution of the species by counties. The distribution of I. pallida is more localized and, in general, is confined to the more southerly counties of the state. The spotty distribution on the map is due to the fact that a comprehensive study of distribution has not been made. A thorough search would probably reveal the presence of both species throughout the southern counties and perhaps in some additional isolated areas in the northern counties.

The discovery of I. pallida on the Red Lake peninsula, Beltrami County by Dr. M. F. Buell (personal communication) was especially interesting. He found both Impatiens species growing on the recently cut-over area which had been covered with a deciduous forest in an otherwise conifer region. The occurrence of I. pallida here led to the conclusion that it must be closely associated with deciduous forests.

The general appearance of the plants is one of luxuriance. The leaves are large and numerous, and the stems are highly succulent. There is a considerable variation in height within the two species, but under favorable conditions both species may be well over a meter high, and three centimeters in diameter at the base. The stem is straight and hollow, but is sometimes closed at the prominent nodes (Meyer and Walker, 1951). It tapers

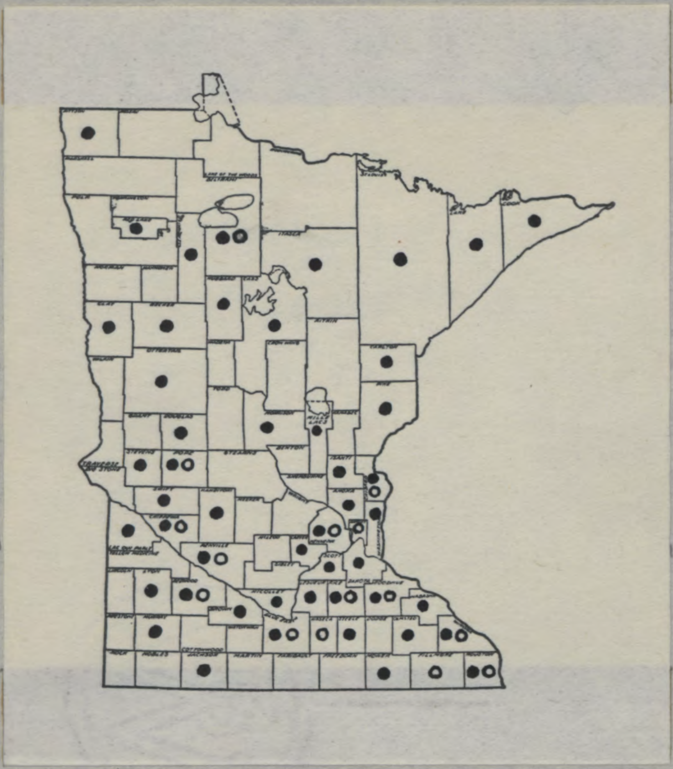
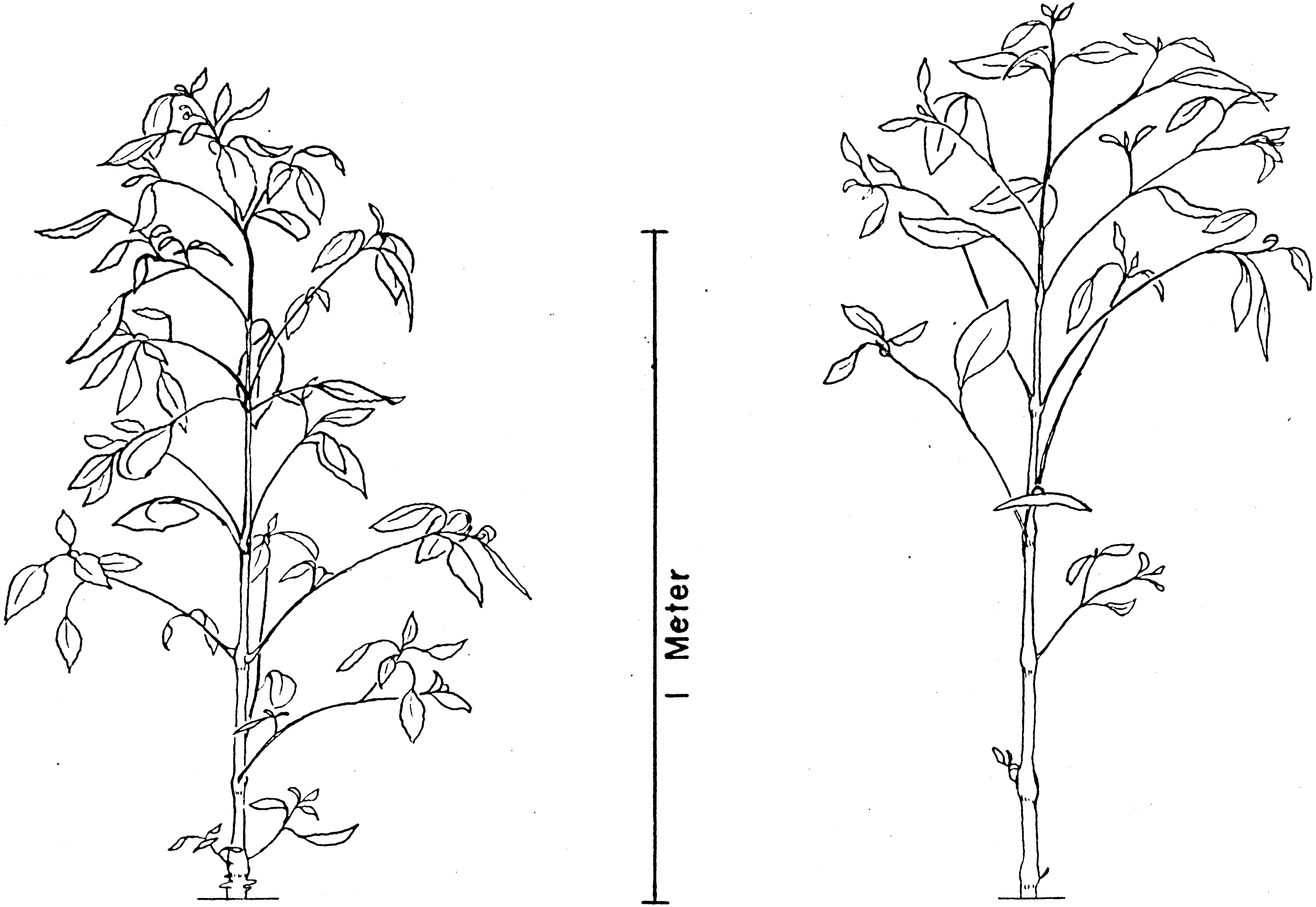


Figure 2. Minnesota showing distribution of Impatiens by counties. The solid circles indicate I. biflora; the open circles indicate I. pallida.

gradually to the apex. Some of the leaves are opposite while others are alternate. Branches arise from the axils of most of the leaves. A single I. biflora plant when not too crowded by other plants has its longer branches located near the base, while I. pallida has its longest branches located farther up on the stem. Figure 3 shows the two species drawn to scale. The appearance of dried plants is different for the two species. I. biflora stems tend to shrivel more, indicating that the amount and distribution of parenchymatous tissue and fibers is different from I. pallida.

The roots are sparse and entirely adventitious in mature plants. Adventitious roots frequently appear several nodes above the surface of the ground, particularly in I. biflora, especially if the plant is growing in deep litter or if it has fallen over so that the nodes come in contact with the soil. Studies were made of the appearance of the roots of I. biflora from various habitats at Itasca Park, but no significant variations were found.

A complete study of the anatomy of I. pallida has been done by Meyer and Walker (1931), but in their study no emphasis was placed on the influence of the environment or the adaptation of the plant to its habitat.



IMPATIENS BIFLORA IMPATIENS PALLIDA

Figure 3. Two species of *Impatiens* drawn to scale.

II. HABITAT

Studies were made of some of the characters of the habitat in order to discover the range of environmental factors that could be tolerated by the plants.

I. pallida can be said to be characteristic of the mature floodplain community. The subclimax forest community of Minnesota floodplains consists mainly of *Acer saccharinum* and *Ulmus americana* with some *Acer Negundo*, *Ulmus fulva*, *Populus deltoides*, *Fraxinus nigra*, and *Celtis occidentalis*. The shrubs usually present are *Cornus stolonifera*, *Vitis riparia*, and *Evonymus atropurpureus*. The herbaceous ground cover is *Laportea canadensis*, *Galium Aparine*, *Impatiens pallida*, *Urtica gracilis*, *Urtica dioica*, *Carex gracillima*, *Cryptotaenia canadensis*, *Hydrophyllum virginianum*, and *Elymus virginicus*.

The seedlings of *Impatiens* are especially conspicuous in the early spring when the large, blue-green cotyledons are emerging. The developing plants must compete with other moisture and shade tolerant species which grow near them. Figure 4 shows the receding waters of the Minnesota River on the floodplain at Ninemile Creek. The chief competitor of *I. pallida* is probably *Urtica dioica* (nettle) which is a perennial that grows to about the same height as *I. pallida*. The climate and seasonal fluctuation of the river level of some years favors *I. pallida*,

Figure 4. Floodplain at Ninemile Creek, May 4, 1947, showing receding flood water. The small plants emerging from the shallow water are nettles. Seedling *Impatiens* plants, which had already appeared before the flooding, are mainly still submerged. (Photo by Dr. Lawrence.)

enabling it to flourish in almost pure stands on the floodplain floor where the loose rich soil becomes very well drained and aerated as soon as the spring flood has receded. Needless to say, the study of *Impatiens* becomes uncomfortable when ~~*Laportea*~~ *Urtica* is abundant.

No *I. biflora* was found on the floodplain proper at Ninemile Creek or Fort Snelling, although it grew in isolated patches in the muck of neighboring springs. It was abundant, however, in the bogs and bog forests of both Itasca State Park and Cedar Creek Forest where *I. pallida* has not been found.

In general, both species of *Impatiens* grow most commonly in the shade of a forest canopy, but both may grow in full sunlight provided there is an ample supply of soil moisture which can be supplied at a rapid rate. Those plants which grow in open sunlight without competition have a different appearance from shade-grown plants. Figure 5 shows the difference in appearance of sun-grown and shade-grown plants of the two species. The sun-grown plants were collected from a gravel bar in the Apple River Canyon, Wisconsin; the shade plants grew on muck soil about 50 feet away. The photograph shows that the sun-grown plants are shorter and more compact, have rapidly tapering stems, and have more numerous roots.

Several counts were made on the density of mature (i. e., with flowers) *I. pallida* and *I. biflora* plants per

1 2 3 4

Figure 5. Comparison of sun-grown and shade-grown species. Nos. 1 and 2 are I. biflora; Nos. 3 and 4 are I. pallida. Nos. 1 and 3 are shade-grown with competition on moist muck. Nos. 2 and 4 are sun-grown without competition. (Photo by Dr. Lawrence).

square meter in the densest colonies that could be found. Table II shows the results of counts in several different areas. In each case the counts were made in an area where the plants were growing in almost pure colonies, and were of uniform size and density within the square meter. Mature I. biflora was noted growing in dense groups of from ten to twenty plants in which the stem bases were touching one another and the roots were tightly interlaced. They were also found growing in close proximity to other species. Mature I. pallida was not observed growing in such a situation although tight clusters of that species were found in the seedling stage. These clusters will be discussed in the section on seedlings. From these data and other observations, it was concluded that I. pallida requires much more area for attainment of maturity than I. biflora; this striking difference may be related to difference in available soil moisture in the habitats in which they usually grow.

The contribution of these herbaceous plants to the litter of the forest floor was studied as a measure of the organic productivity of annual parts as compared with that of all the other forest species. Collections of litter were made from three one meter square quadrats on the floodplain at Fort Snelling, after the first heavy frost which ended the growing season for Impatiens. Each quadrat was located in an area where I. pallida was growing

Table II. Adult density of the two species of *Impatiens* within the densest stands.

Location and Year	*I. biflora* Number per sq. meter quadrat	*I. biflora* Number of quadrats	*I. pallida* Number per sq. meter quadrat	*I. pallida* Number of quadrats
Ft. Snelling floodplain, 1947	--	--	30	1
Ninemile Creek floodplain, 1948	--	--	8-30	11
Itasca Park shrub-sphagnum, 1947	150-700	17	--	--
Itasca Park bog forest, 1947	120-900	17	--	--
Average	369	--	16	--

in dense stands. The litter was separated into two groups: *I. pallida* parts, and all other undecomposed organic matter which included mainly tree leaves. It was dried in an oven at 105° C. for two days, and then weighed. Table III shows the values obtained. *I. pallida* contributes from 19 per cent to 39 per cent of the dry weight of the litter of areas in which it is growing at near its maximum density. Similar data for *I. biflora* were not obtained.

Table III. Oven-dry weight in grams of litter from Fort Snelling floodplain.

Group	Quadrat I	Quadrat II	Quadrat III	Total
I. pallida parts	378.9	80.0	131.8	590.7
Other organic litter	590.0	338.6	334.8	1263.4
Total	968.9	418.6	466.6	1854.1
Per cent *I. pallida*	39.2	19.1	28.3	31.9

III. GALL INSECTS ASSOCIATED WITH IMPATIENS

Observations were made on the insects infesting both species. Two types of galls were found on *I. biflora* at Itasca. One type, forming one centimeter long translucent bulges, was noted on the petioles and midribs of the leaves of nearly every plant, although its effect on the vigor of the plant appeared to be minor. I noticed the same type of gall on *I. pallida*, but it is rare. The other type of gall found at Itasca was located in the buds, which were distorted and greatly enlarged. Both of these galls are discussed by Felt (1940) and Lutz (1935). They are formed by two minute and economically unimportant, dipterous insects of the family *Cecidomyiidae*, commonly known as the gall-gnats. The petiole and midrib gall is formed by *Lasioptera impatientifolia* Felt, and the bud gall is formed by *Cecidomyia impatientis* O. S.

IV. SOIL AERATION

Since field observations of the two species had shown that I. biflora was found frequently in soils that appeared to be lacking aeration, whereas I. pallida was usually found on soils well aerated at least after the spring floods had passed, it was thought that soil aeration might be one of the important factors in determining the distribution of the two species. An experiment was devised to test the ability of the two species to survive in poorly aerated culture vessels. Figure 6 is a diagram showing the aeration apparatus and the culture vessels. Explanations for the various parts of the apparatus are given under the figure. The vessels were numbered from one to twelve; those numbered 1, 3, 5, 8, 10, and 12 received air. The experimental design was such that I. biflora and I. pallida plants were arranged to provide aeration for half the plants of each species. However, through a mistake in identification, the plant in vessel 4 was actually I. pallida instead of I. biflora as intended. The "P" and "B" on the vessels indicate the arrangement of the species as the experiment was actually carried out, using seven I. pallida plants and five I. biflora plants.

The experiment was set up in the following way. The pump (A) was a Cornelius model K compressor. The T tube

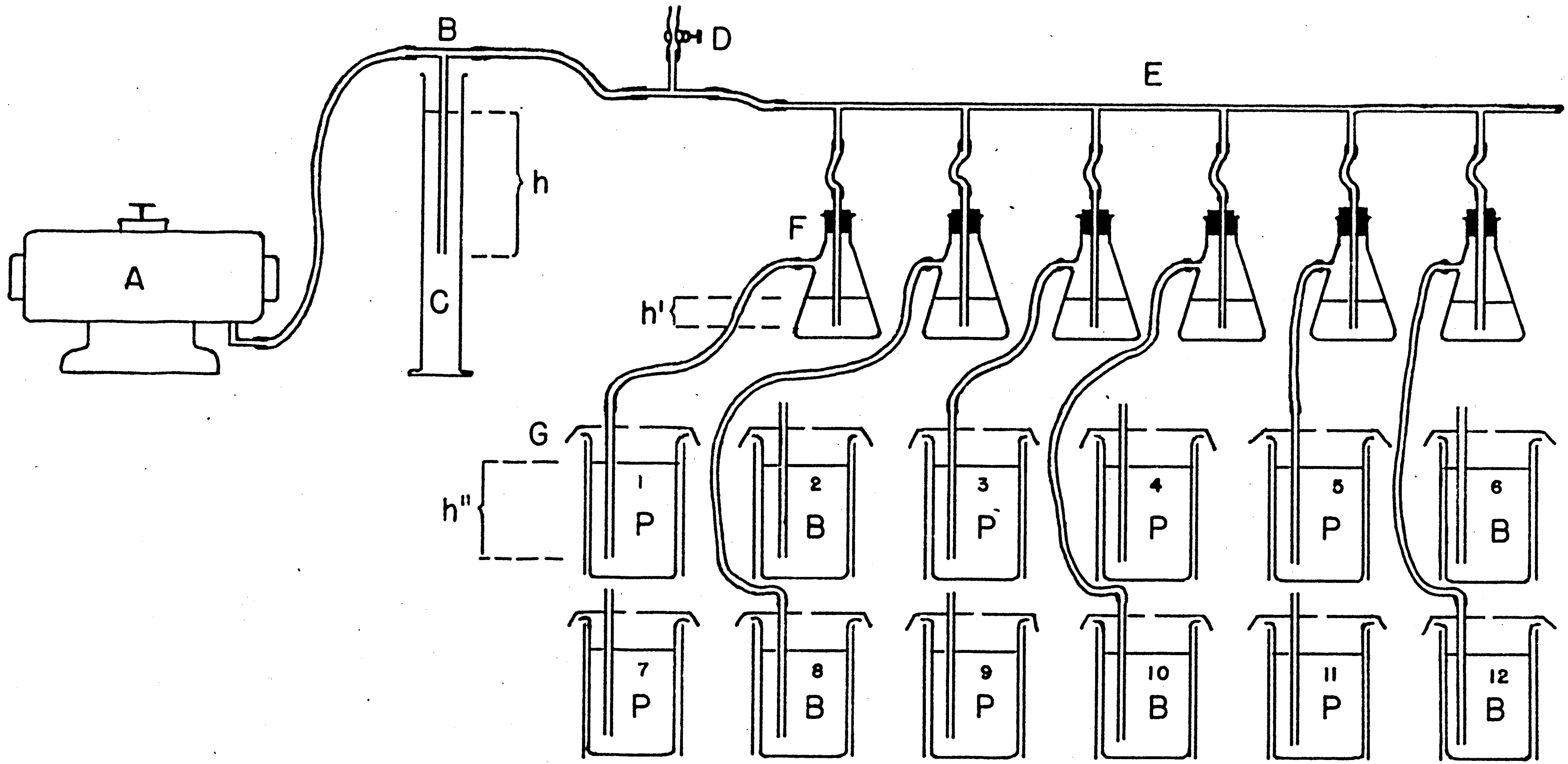


Figure 6. Diagram of aeration apparatus (plants not included). A, pump; B, long T tube; C, cylinder with water at height h; D, outlet provided with a screw clamp; E, manifold; F, flasks with water at height h'; G, culture vessel with water and soil mixture at height h"

(B) in the cylinder of water (C) was used to assure a continuous and even stream of air to all of the culture vessels. The height h was adjusted so as to be slightly greater than the height h' plus h". The outlet (D) was adjusted also until air was bubbling at the desired rate through the cylinder. As long as there was enough pressure to force bubbles through the water in the cylinder, then it could be assumed that air was bubbling through all of the culture vessels. Each culture vessel (G) was a narrow (9 cm. diameter), one liter beaker with a stiff paper cover over the top and a cylinder of corrugated cardboard around it. The paper on the top had two holes, one in the center and the other to the side. The stem of the plant passed through the center hole and was supported by the paper and a little wad of cotton. The aerating tube passed through the side hole. The half-grown plants, about 20 cm. tall, which were used in the experiment were selected for uniformity of size and vigor, from a small population located around a pond adjacent to the University of Minnesota Botany greenhouse. Each plant was removed by placing a tin can, minus its top and bottom, vertically slit down the side to admit the stem, and of the same diameter as the culture vessels, around the base of the plant. The can was pushed down into the soil and the whole plant with the cylinder of soil around the roots was removed and placed into the culture vessel. Tap water was added over the soil. The aerating tube was inserted deep enough to penetrate the soil at the bottom of the beaker. During aeration, the soil was churned up and mixed with the water. It was assumed, on the basis of work by Lönnerblad (1930) and Lindeman (1942), that the micro-organisms of the soil in the unaerated cultures reduced the oxygen concentration to practically zero within a few hours of the start of the experiment.

The experiment was carried out on a bench in the Botany greenhouse during the first week in August. It was continued for one week, after which notes were made on the condition of the plants. Table IV shows the condition of each plant at the end of the experiment. Plant number 9, which showed no visible change, was an exception which might have been due to the somewhat older nature of the plant, when the experiment was started, or, more likely still, to an inherent difference in genetic and physiological constitution. It might have showed some change if the experiment had been continued for a longer period. The death of plant number 6 may have been caused by damage to the roots when the plant was removed from the soil.

Although the results of this single experiment are not conclusive, they do seem to indicate that there is a distinct difference in the behavior of the two species. I. biflora has the ability to form adventitious roots on

Table IV. Condition of plants after aeration experiment.

Vessel No.	Species	Air	Condition
1	<u>pallida</u>	+	No visible change in appearance
3	"	+	No visible change in appearance
5	"	+	No visible change in appearance
4	"	-	Dead
7	"	-	"
9	"	-	No visible change in appearance
11	"	-	Dead
8	<u>biflora</u>	+	Adventitious roots
10	"	+	" "
12	"	+	" "
2	"	-	" "
6	"	-	Dead

nodes several internodes removed from the base of the plant. No adventitious roots were found on I. pallida plants. The ability to form adventitious roots far up on the stem above the surface of the oxygen-free substratum might well be an important factor in the development to maturity of the species in a soil lacking in sufficient oxygen. Further experimentation with many more plants would be necessary to prove this point.

V. FLOWERS, FRUIT, AND SEED PRODUCTION

Both showy and cleistogamous flowers are found on the two species of Impatiens. The showy flowers of both species have essentially the same structure. The floral formula for the family Balsaminaceae, of which Impatiens is the principal member, is given by Pool (1941) as follows:

$$\frac{\mathrm{Caz}^{3-5}\ \mathrm{Coz}^{3-5}\ \mathrm{S}^{\widehat{5}}\ \mathrm{P}^{\textcircled{5}}}{\mathrm{Cap\ Bac}}$$

He describes the flowers as "...perfect, hypogynous, zygomorphic, brightly colored, solitary or somewhat umbellately clustered; sepals 3, rarely 5, unequal, the two lateral ones small and greenish, the posterior one prolonged backward into a nectariferous, tubular spur; petals 5, or 3 by the union of two pairs, unequal; stamens 5, filaments short and broad, anthers connate around the ovary; ovary superior, five-celled, with few to many ovules in each cell; fruit a succulent capsule or berry, with several seeds; endosperm 0." The differences in the color of the flower and the shape of the tubular sepal of the two species were given in Table I.

Observations were made on the number and position of cleistogamous flowers as opposed to showy flowers of I. biflora on two plants (A and B) growing at the edge of the pond by the Botany greenhouse of the University of

Minnesota. The first showy flower to open was noted on June 30, 1948, on the end of one branch of a pedicel located ten nodes above the base of plant A which had eighteen visible nodes at that time. Another flower was found at the eleventh node from the base of plant B which had seventeen visible nodes. On both plants there were a number of other buds far enough advanced to be definitely recorded as showy flowers (see Table V). Other plants were observed that had one or more open showy flowers located on branches on the upper part of the plant. At the same time (June 30) that the first showy flowers were observed, other plants were examined for evidences of cleistogamous flowers. On the lower branches many buds were noted. Several immature fruits were found also which had not been preceded by showy flowers, and which were presumed to be the result of development from cleistogamous flowers.

Two and five days later the two plants under observation were examined again. During that time no more showy flowers opened, but the number of showy flower buds increased. It was found, however, that during the total five-day period many fruits developed to a recognizable, but immature, stage where only buds had been present before. The one showy flower which had been present on each plant had also been replaced by fruit which was still immature. It was impossible to tell from external appearances of

Table V. Number of showy flowers or showy flower buds and cleistogamous flowers found on two *I. biflora* plants for a five-day period.

	June 30		July 2		July 5	
	Plant A	Pl. B	Pl. A	Pl. B	Pl. A	Pl. B
Showy	5	13	7	28	5	26
Cleistogamous	6	14	5	19	3	12
Ratio of showy/cleistogamous	.83	.93	1.4	1.5	1.7	2.4
Average ratio	.88		1.5		2.1	

the young bud whether a flower would be cleistogamous or showy. The ratio of the number of showy to the number of cleistogamous flowers was calculated for the five days. Table V shows the numbers obtained. The figures show that the ratio increased during the five day period. I. biflora was observed later in the summer with an abundance of showy flowers. Presumably, the ratio continues to increase as the summer progresses and the plants mature. According to Blanchan (1916), in England where I. biflora is rapidly becoming naturalized, Darwin recorded a ratio of 20 plants producing cleistogamous flowers to one having showy blossoms, which even when produced, seldom set seed. Blanchan attributes this lack of seed set by showy flowers in England to the absence there of hummingbirds which he considers the most important agent of cross pollination of this plant in North America, though he says that the flowers are also visited by bumble bees. He says it is estimated that each flower produces about 250 pollen grains. The writer observed both hummingbirds and bumble bees obtaining nectar from I. biflora flowers at Itasca.

No studies were made on the appearance of flowers of I. pallida, but it was noted that I. pallida seldom has as many showy flowers as I. biflora. Hanes and Hanes (1947) observed fully developed seed pods on I. pallida 12 to 15 inches high on June 15, 1946 in Kalamazoo County, Michigan, while on plants 2 to 3 feet in height they were lacking.

Raitt (1946) who has studied the development of the ovule of I. pallida reported that cleistogamous flowers appear late in May and continue through June with some continuing through the summer along with the normal flowers.

It seems obvious from the observed production of both cleistogamous and showy flowers in these two species, that seeds of two genetic makeups are produced, the ones from the cleistogamous flowers, being self-pollinated, should be genetically more uniform than those from the cross-pollinated showy flowers. This may be responsible for the tremendous variation in size and apparent vigor within local populations of seedlings that have been seen in Minnesota. It would be interesting also to learn whether the ratio of showy to cleistogamous flowers is influenced by climatic conditions as well as by the stage of development of the plant.

The fruit of Impatiens is the most distinctive and characteristic organ of the plant. It is the part of the plant which has given it both the botanical and common names. The releasing mechanism of the fruit, which scatters the seeds, has been investigated by several workers (Brunotte 1896, Pfeffer 1900, Guttenberg 1926). It has been concluded by them that differences in cell growth and structure are responsible for strains produced in the developing fruits. Apparently the cells of the outer layers of the carpels grow more rapidly than those of the inner layers. When the fruit reaches maturity, the sutures between the carpels become very loosely connected. The fruit itself is only loosely attached to the receptacle. The slightest disturbance of the fruit causes the carpels to separate from one another and from the receptacle, and to curl inward very rapidly. The general effect is a rapid snapping movement during which carpels, seeds, and placenta separate and are scattered to a distance which, according to Blanchan, may be as much as four feet in I. biflora.

The first mature fruits on I. biflora were noted about the middle of June. The mature fruits of I. pallida were found about two weeks later. Both species continue to produce seeds throughout the summer, and until the first killing frost.

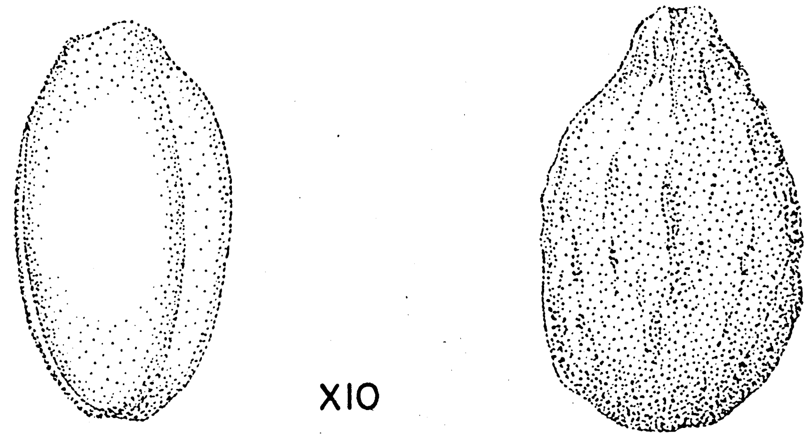
Fifty fruits of I. pallida were examined for numbers of seeds. Fifty per cent had one seed, 44 per cent had two seeds, and 6 per cent had three seeds. In I. biflora, the majority of fruits had three or four seeds with occasionally two.

When the seeds are liberated from the fruits they are usually green with blotches of brown on them. They may be still entirely green with a soft seed coat. Those that are green when liberated start immediately to turn brown and are entirely brown within a few hours. Green seeds have been found on the ground which were liberated by "natural" means (i. e., not by the writer). It is presumed, then, that they were not released by immature fruits.

Figure 7 shows the seeds of I. biflora and I. pallida. Those of I. biflora are the smaller of the two species. They are of a uniform, dark, gray-brown color, smooth, sometimes glossy, and with four prominent ridges running lengthwise. The seeds of I. pallida, in addition to being larger, have a somewhat blotched appearance and a rough surface. The ridges are absent.

At the time of dispersal 38 seeds of I. biflora had an average weight of 0.0063 grams; 236 seeds of I. pallida had an average weight of 0.0201 grams.

Salisbury (1942) has studied the relation of seed weight to habitat. He found that with increasing density of the shade of a plant community there is an increase in seed weight. He states that "...in general the larger the supply of food material provided by the parent plant in the seed, or other propagule, the more advanced the phase of succession that the species can normally occupy." Table VI is a portion of a table prepared by Salisbury showing average seed weights for various habitats. I. biflora is close to the values he obtained for meadow or scrub species while I. pallida is closer to the values for shade species. If Salisbury's conclusions are correct, then the two species of Impatiens can be considered typical



IMPATIENS BIFLORA IMPATIENS PALLIDA

Figure 7. Seeds of *Impatiens*.

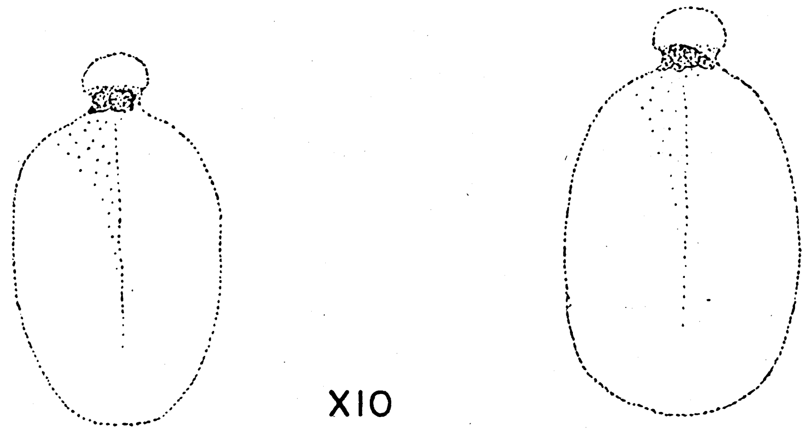
Table VI. Summary of average seed weight (in grams) of herbs of various habitat conditions. (From Salisbury, 1942).

	Open habitat	Semi-closed or closed non-shady habitats	Meadow	Scrub & wood margin	Shade species
No. of species	70	22	8	32	27
Average weight	0.00119	0.002214	0.0049	0.004438	0.013686

of different habitats; my observations indicate that this is true.

Figure (8) shows the inner surface of a single cotyledon of each species as it appears when removed from the mature seed. The radicle appears as a knob at the end of the cotyledons. No plumule is visible. The entire embryo of the living seeds of both species is a striking sky-blue color, but the pigment has not been identified.

Measurements were made for I. pallida of the length and width of the living embryos immediately following dispersal; at that time the embryo completely filled the seed and no endosperm was visible. The average length of the cotyledons was 4.4 mm., width 3.3 mm., and length of radicle 0.7 mm. Dimensions for I. biflora would be somewhat smaller, but no measurements were made of the embryos of this species.



IMPATIENS BIFLORA IMPATIENS PALLIDA

Figure 8). Inner surface of the cotyledons of <u>Impatiens.</u>

VII. STORAGE AND GERMINATION

No germinating seeds or seedlings were found during the summer or autumn of two successive years. A certain period of time must elapse after dispersal before the seeds become able to germinate. Just what chemical changes go on within the seed during this period of after-ripening are not known at present, nor is it known what exact conditions of the environment are necessary to allow these changes to take place. It has not been discovered, for example, whether _I. pallida_ requires a freezing period before germination can occur.

Some seeds of _I. biflora_, derived from a colony native at Cedar Creek Forest germinated without having been exposed to freezing temperature. Dr. Lawrence (personal communication) found, in the spring of 1948, a few etiolated seedlings of this species which had germinated in darkness on the wall of a wooden tub containing water lily plants rooted in saturated soil, and which had been stored for the winter in a cool basement where no freezing had occurred. The seeds had at first been submerged in about two inches of water and later been merely in a saturated atmosphere. The seeds had never had a chance to dry out from the time of dispersal when the seeds had fallen directly into the pond in which the water lily had been growing.

Seeds of _I. pallida_ were collected by hand directly from the unopened, but mature, fruits at Ninemile Creek on September 20, 1947. They were stored in an envelope at room temperature and humidity for one day. They were then divided into six lots and each lot was subjected to a different storage condition (Table VII) in order that the effects of these storage conditions on the germination of the seeds could be ascertained. Each lot was placed in a 1/2 pint Mason jar which was covered with a clamped-on glass top and sealed with a rubber jar ring. They were all placed in the refrigerator at 7° C. except two, one of which was placed in the freezing compartment at -0.5° C. The other one was placed outside, adjacent to the pond by the botany greenhouse where there is a natural colony of both Impatiens species. The outside jar had a hole in the bottom and was half filled with moist soil. The seeds were placed on the surface of the soil in the jar. This jar was also covered with a glass top sealed with a rubber ring. It was then placed in the moist soil with its top even with the soil surface. After one month of this storage, five seeds were removed from the jar and their embryos were measured as before. There was no significant difference in size of the embryos after one month of storage. There was also no change in the gross appearance of the embryos.

Some seeds of I. biflora were stored also. These seeds had been collected by Dr. Lawrence from his garden

Table VII. Storage conditions of *I. pallida* seeds.

Lot	Storage Condition	Temperature and Location
A	Under surface of muck*	7° C. Refrigerator, lower shelf
B	On moist soil surface	7° C. Refrigerator, lower shelf
C	On moist soil surface in jar with hole in bottom	Outside
D	On moist soil surface	-0.5° C. Refrigerator, freezing compartment
E	Suspended above fused $CaCl_2$, 32% R.H.	7° C. Refrigerator, lower shelf
F	Suspended above distilled water	7° C. Refrigerator, lower shelf

* Muck from bottom of Botany greenhouse pond.

on September 22, 1947. Some were picked by hand directly from plants derived from the population at Cedar Creek Forest. These seeds were stored air-dry in a manila paper envelope outdoors on a west window sill until November 22. They were then brought indoors and placed on saturated cotton. They were kept at room temperature during the storage period. They started to mold the second day after being put on the cotton, and the embryos gradually decayed. Presumably the seeds had lost their viability. Another group of I. biflora seeds was also collected by Dr. Lawrence from a pond in his garden where they had remained submerged since dispersal; these were also placed indoors on moist cotton. They showed very little mold even after several months, but they did not germinate. The embryos remained sound and were presumably viable. The two groups of I. biflora seeds were kept moist with distilled water and at room temperature until the germination test described below.

On January 24, 1948, after four months of storage, the I. pallida seeds which the writer had stored outside and in the refrigerator, and the I. biflora seeds which had been collected by Dr. Lawrence were tested together for germinating ability. According to Weather Bureau data, the outdoor temperature during the four months ranged from 88° F. to -21° F. Before the seeds were planted, five of the I. pallida seeds from outside were measured. Again, there was no significant change in the size of the embryo.

The germination test was carried out in the following way. Twenty-four seeds of each lot were buried two millimeters deep in a greenhouse flat of loam soil. The flat was placed under a bench in a cool greenhouse about 10 inches below a bank of 40 Watt daylight flourescent lights placed parallel with each other and spaced 10 inches apart. Interspersed halfway between each pair of tubes was a row of four 25 Watt Mazda tungsten bulbs. Low intensity, diffuse light also entered the growth chamber during daylight hours, but no direct sunlight. An automatic timer was connected to the lights and set to turn them on at 5:30 A. M., and off at 7:00 P. M., thus providing a 13 1/2 hour photoperiod, which simulated the lighting conditions of the first week in April when the first seedlings of _I. biflora_ were found in the field. Two maximum-minimum thermometers were placed on the edge of the flat, exposed to the air and artificial light. The average daily maximum temperature during the experiment was 24° C., and the average daily minimum temperature was 9° C. The highest temperature reached was 31° C., and the lowest was 4° C. The soil of the flat was kept moist by periodically lowering it into a pan of water to enable the soil to absorb water through the cracks in the flat.

Seventeen days after the seeds were planted, the first seedlings appeared. These were from I. pallida seeds which had been stored outside; 9 out of the 24 seeds germinated over a period of 19 days; though the experiment was continued for 20 days longer, no more seeds germinated. The final germination per cent for the seeds stored outside was 37.5. None of the refrigerator-stored I. pallida or the I. biflora seeds stored moist at room temperature germinated. These results indicate that the after-ripening of I. pallida can occur in four months or less when exposed to outdoor winter conditions. Seedling clusters, which will be discussed in the next section, were collected during the middle of May, 1947, and counts were made on the number of ungerminated seeds present. Of three clusters containing 29, 136, and 278 seeds and seedlings, the per cent of germinated seeds was respectively 100, 95, and 81. These per cents are seen to be much higher than those obtained in the germination test, indicating that a longer period of outdoor storage can raise the germination per cent to a much higher level.

After the germination test, as many seeds as could be found were recovered from the flat and their embryo sizes measured as before. About half of the I. pallida planted were recovered, but none of the I. biflora seeds. The recovered seeds were sound, but presumably after-ripening had not progressed sufficiently to allow germination. The blue color of the cotyledons and the size of the embryo were the same as before except for a possible slight increase in length of the cotyledons.

Meyer and Walker (1931) in their study of the vegetative anatomy of I. pallida found that seeds collected from the soil about the middle of March and sectioned showed secondary roots that had already formed, but were still within the radicle. Just before germination they became more definite, and pushed through the cortex immediately after germination. The authors included no description of the seed at the time of dispersal, but it is conceivable that the development of secondary roots may be necessary before the seed will germinate. This development would undoubtedly be closely associated with physiological changes which must proceed during exposure to winter environmental conditions.

VII. SEEDLINGS

It is difficult to distinguish the seedlings of I. pallida from those of I. biflora. A difference in size of the cotyledons was noted in some cases, but it was considered doubtful whether this difference between the two species was constant enough to be useful in identification. Statistical studies on large numbers of seedlings from various habitats would probably show some differences, but would be useless in the identification of any one individual. The best method for identification of seedlings was found to be not the seedling itself, but the seed coat. A careful search near the base of the seedlings usually reveals the seed coat, which is very distinctive for the two species (Figure 7).

The earliest I. biflora seedlings of the year 1947 were found on April 19. They were sprouting from saturated soil along a small stream which emerged as a spring from a southeast facing hillside near the floodplain at Ninemile Creek. I. pallida seedlings were found on May 3, fourteen days later, on the floodplain proper where the soil was moist, but not saturated.

The earliest seedlings of the year 1948 were found on April 3; these were I. biflora. Like the previous year they were growing in saturated, sandy muck with their roots in the slowly running water of a small spring-fed stream on a south-facing hillside, 1/4 mile upstream (on Ninemile Creek) from the stream in which the first seedlings of the previous year were found. The temperature just under the surface of the muck in which they were growing ranged from 6.5° C. to 9.0° C. The muck may have remained above freezing all winter, because of the constant flow of warmer ground water. The temperature of the air at that time was 3.0° C. The temperature just under the surface of the soil on the hillside, which was comparatively dry and in which no Impatiens seedlings were growing, was 6.0° C. The temperature of the soil under the overhanging, north-facing bank of the small stream was 4.0° C.

One week later, April 10, seeds were still germinating in the same small creek. At that time the temperatures of the muck varied from 9.0° C. to 11.0° C. The air temperature was 12.5° C. The temperature of the same hillside above the stream varied from 11.5° C. to 13.5° C. At this time temperatures were taken on the floor of the floodplain proper at Ninemile Creek in a place where there were many dead plants of what were known from the previous summer to have been I. pallida. No seedlings of this species were found then. The temperature of the soil was taken on the same day (April 10) and did not differ greatly from the temperature of the hillside stream. It varied from 9.5° C. to 10.0° C. The soil was comparatively dry, but there were places where water was standing in slight depressions. The temperature of the water in these depressions varied from 9.0° C. to 12.5° C. No *Impatiens* seedlings were found either in or near these depressions, or on the higher soil surface.

The following week, April 17, the temperature of the muck at the hillside stream was 9.0° C. which was also the temperature of the floodplain proper. The air temperature at that time was also 9.0° C. *I. biflora* seedlings continued to appear, but no *I. pallida* seedlings were observed.

The next week, April 24, three weeks after the appearance of *I. biflora*, *I. pallida* seedlings were observed for the first time and were abundant. The temperature of the soil in which they were growing varied from 16.5° C. to 20.0° C. There were no *I. pallida* seedlings growing near the standing water in the depressions, which was 19.0° C. Some *I. pallida* seedlings were also found for the first time on a south-facing bluff above the floodplain. The temperature of the soil there was 18.5° C.

From the temperature readings around germinating seedlings of both species, it appears that *I. pallida* requires a higher temperature for germination than *I. biflora*. It is apparent from these studies that the water content of the soil is not the limiting factor, for even when water is abundant seeds of *I. pallida* did not germinate until the soil temperature was between 15° C. and 20° C. Soil aeration, however, is another factor which may effect the germination of the seeds. The lack of sufficient aeration may explain the absence of early seedlings around the water-filled depressions, and *I. pallida* may have a much higher oxygen requirement than *I. biflora*, although the oxygen concentration of the surface layers of the soil at that time of the year would probably not be very low, due to the relatively low temperature and the lack of decomposing organic material.

The ability of the seedlings of *I. pallida* to survive after flooding is an important factor in growth on the floodplain. Four stations were established on the floodplain at Ninemile Creek, each station having *I. pallida* seedlings near it at one time or another. The spring flood of 1947, which occurred approximately one week after the seedlings were first noted, covered three of these stations for varying numbers of days. Table VIII shows the condition of the seedlings after flooding. The table shows that many seedlings can survive flooding if the duration of the flooding is not too long. Only 50 per cent survived submergence for seven days and none survived submergence for ten days. They also have the ability to survive extensive damage to their cotyledons, as is shown by the fact that three seedlings which had lost their cotyledons and were thought to be dead

Table VIII. Condition of seedlings after flooding.

Station	Days under water	No. of seedlings 0 days after flood (5-13-47)			No. of seedlings 4 days after flood (5-17-47)			No. of seedlings 11 days after flood (5-24-47)		
		Dead	Total	% Alive	Dead	Total	% Alive	Dead	Total	% Alive
A	0	0	5	100	0	5	100	0	5	100
C	7	12*	32	63	12	32	63	16	32	50
B	10	16	16	0	0	0	0	0	0	0
D	12	0	0	0	0	0	0	0	4†	100

* Three other seedlings thought to be dead, later revived although their cotyledons had dropped off.

† These were seedlings which did not appear until after the flood had receded.

immediately after the flooding, survived through the eleven-day period of observation. No seedlings were found at station D, even before the flood, for on April 24, at the time when the first *I. pallida* seedlings were found at the other stations, flood water had already risen over station D. Seedlings did not appear there until May 24. It is possible that seeds were late in germinating there, because the cold flood water must have chilled the soil at that station. There were usually fewer numbers of *I. pallida* plants in that area.

A very striking feature of the seedling stage of *Impatiens* is the frequency of aggregation of seedlings into clusters. The clusters are usually ten to twenty centimeters in diameter (Figure 91) and may contain as few as 20 or as many as 200 seedlings, so closely spaced that the stems are often in contact. Excavation of a cluster of very young seedlings reveals many additional sound seeds still ungerminated. The cause of these clusters is unknown. Pure clusters of *I. pallida* and also of *I. biflora* have been found, but it is not known whether a mixture of the two species ever occurs within a single cluster.

The existence of the clusters has been noted in a wide variety of habitats over a period of several years by Dr. Lawrence (personal communication). They have been found in the bog forest at Cedar Creek, in the subclimax

Figure 91. Cluster of I. *pallida* seedlings at Ninemile Creek. (Photo by Dr. Lawrence.)

forest at Ninemile Creek, and in the gravel ballast between railroad ties in the vicinity of Fort Snelling. The discovery of apparently similar clusters in a place recently flooded by the Minnesota River leads the writer to guess that the clusters might have been deposited by eddies in the flood waters, but several of the sites mentioned above are never flooded. Since the mature fruits of the plant never contain more than four seeds, and the whole fruit explodes at maturity, projecting the individual seeds a distance of several feet, the germination of seeds within an intact fruit cannot be responsible for the clusters. It is possible that some animal might collect the mature seeds from the soil surface after dispersal and bury them in groups. Rodents have the characteristic habit of collecting and caching seeds of certain plants. Some rodent is therefore strongly suspected of the grouping of the seeds that later develop into the seedling clusters.

In the spring of 1947, a count of the spacing of clusters was made on a 400 square meter plot at the Ninemile Creek study area on land that had not been flooded for at least ten years. 28 clusters were found. The following spring (1948) was unusual for the very small number of clusters found in all habitats, and none of them were found in the same area studied in the spring of 1947. No explanation can be offered for the difference in the number of clusters in the two years except that the fall of 1947 was one in which warm, sunny weather continued throughout October, with the result that the average temperature for that month was 10° F. higher than normal. This warm fall ended with a sudden severe storm with snow and below-zero weather. One or another of these unusual weather features may have had some effect on the seed-gathering or seed-consuming habits of the suspected rodents. Only a few seedling clusters were found in the whole Ninemile Creek study area in the spring of 1948. Those that were discovered were very close to the bases of trees in which there were holes obviously inhabited by rodents.

In the spring of 1940 Dr. Lawrence (personal communication) made a few careful observations on seedling clusters in the area lying between the old water tower on the bluff at Fort Snelling, and the edge of the Mississippi River below. On May 5 he marked four clusters in habitats ranging from very dry ones to ones where the soil was thoroughly saturated. Station No. 1 was at the edge of the railroad track. Stations No. 2 and No. 3 were in a spring-fed moist area of muck inhabited by skunk cabbages. Station No. 4 was on the dry dredging gravel of the river levee. Observations on another cluster were begun later (May 23) at a station (No. 5) also on the gravel levee. Observations and recounts were made at convenient intervals through the growing season. The results are shown in Table IX.

The observations brought out the great mortality of plants in the clusters. Unfortunately, no observations for comparison were made on mortality in solitary individuals, but it is thought that deaths of them were very much fewer. Competition for moisture and nutrients, between the individuals of a cluster must be very great. It must be kept in mind that the counts are gross values and a few ungerminated seeds in the clusters at the early dates may have provided seedling replacements of deaths, causing totals to remain so uniform throughout May. The species contained in these clusters observed in 1940 remains unknown because a way of distinguishing them in the seedling stage had not then been worked out.

Table IX. Fate of <u>Impatiens</u> seedling clusters, 1940.*

Station	May 5	May 23	June 2	Oct 13
	Number and condition of individuals			
No. 1 - Dry	37	25	26 (about 12" tall)	Not found
No. 2 - Moist	20	21	21 (about 12" tall)	All have been dead for a long time; apparently none attained maturity.
No. 3 - Moist	65	67	66 (about 12" tall)	All have been dead for a long time; no remnants visible, yet adjacent solitary individuals are healthy.
No. 4 - Dry	9	10	group destroyed	Not found
No. 5 - Dry	No observation	15 (all slightly wilted)	15 (about 4" tall)	One still alive; it had attained maturity, but was black from frost.

* Data supplied by D. B. Lawrence.

DISCUSSION

It is difficult to evaluate a pioneer study of an ecological life history such as this one, because of the absence of other studies to which it can be compared. An attempt will be made, however, to relate the two species of *Impatiens* to their surroundings.

The maps of North America and Minnesota, included in the first section, show that the two species of *Impatiens* have somewhat different geographical ranges, though they overlap to a large extent; that of *I. biflora* is the broader. A large scale map with habitats included would show striking differences. These differences in habitat preference had not been noted before the present study was begun.

There is no doubt that *I. pallida* is closely associated with the mature floodplain, although it is occasionally found in depressions in the forest floor of maple-basswood climax of the region near Minneapolis; it quite definitely occurs on the warmer, dryer soils under a forest canopy. On the Minnesota River floodplain at Ninemile Creek where the most extensive colonies of this species have been found, the level of the water table descends rapidly following the spring flood. Within two months after the flood peak of April 2, 1948, when the water stood 4 inches above the soil at one station, the water table dropped to a level

~~of~~ 41 inches below the soil surface. It remained low throughout the growing season, and the only additional moisture added to the surface of the soil was derived from the summer rains.

As the season progresses and the water table drops, the competition for water becomes more intense. It seems evident, therefore, that between rains, the available soil moisture in the uppermost layers where the forest tree roots draw heavily upon the supply, must be reduced to a critical value for a mesic annual, such as I. pallida. Lack of sufficient water supply for all the plants is probably the major factor in the elimination of many young plants so that at maturity the plants are rather widely spaced. The high mortality of the seedlings in the clusters of I. pallida is probably due, in large part, to the competition for water, and somewhat to the competition for space.

I. biflora cannot be assigned to a particular community; its distribution seems more closely restricted to a rather constant summer moisture supply, for it is usually confined to the margins of permanent springs and streams, and to bogs. It is probably more closely associated with the bog community than with any other single community, but it is certainly not confined to the bog. It is very widespread and more commonly known than I. pallida. Of the two species, I. pallida is the better indicator of dryer, warmer forest soils, while I. biflora indicates a soil with an abundant supply of water throughout the growing season. Since I. biflora almost invariably grows in wetter places than I. pallida, the greater density of mature plants of that species may be due to the absence of competition for water there.

In spite of differences in habitat preferences of the two species, there is no large difference between them in inherent growth form. However, responses to environmental influences such as competition and light intensity can produce marked divergence in growth forms within each species as compared with those I have described above and illustrated in Figure 3. There is a distinct difference between the species in regard to adventitious root formation and survival under the conditions of the experiment on aeration effects: I. biflora produced adventitious roots and could exist at lower oxygen concentration than I. pallida. Under natural conditions these roots have not been observed to such a great extent as in the experiment, but the writer believes that the formation of adventitious roots has survival value. The degree of soil aeration, which would be related to soil water content, is probably an important factor in determining the survival of germinated plants of both species of Impatiens but surely I. pallida to a greater degree.

The species are remarkably free from infestation by insect pests. The two types of galls discussed previously have little effect on the plants; thus insects can be virtually eliminated as a controlling factor in their survival in the Minnesota region.

The succulent stems, thin leaves, and especially the small root system of the two species might indicate that they were not well adapted to drought conditions, and such is the case. They wilt very easily and lose water at a rapid rate, but they will grow well in bright sunlight if the water supply is sufficient. Full sunlight, or various degrees of shading apparently are not important factors in limiting distribution, because both species are found under a thick forest canopy or in the open sunlight.

The number of seeds produced by each plant and the survival of the plants produced from these seeds would give the best indication of the biotic potential that was discussed in the Introduction. It is not possible at this time to give these values since the average number of seeds, which are produced continuously throughout the summer, is still unknown.

The difference in time of germination of the seeds of the two species is probably most dependent on soil temperature, though seed storage conditions may possibly be important also. I. biflora germinates earlier when the soil is cooler. It may be that I. biflora can tolerate lower temperatures throughout its life cycle. Its more northern geographical distribution and occurrence on the cooler soil of bogs and deep shaded canyon floors would be in agreement with its tolerance of cooler temperatures.

Impatiens seedlings are among the first of the annuals to emerge in the early spring and consequently are exposed to many adverse physical conditions. In very early stages, competition from other plants is a minor factor determining their survival except in the seedling clusters, whereas variations in the spring environment can have a strong influence. *I. pallida* can survive flooding following germination providing the flood period is not too prolonged. Sometime between a week and ten days was the limit of time which the seedlings could survive submergence in the spring of 1947. Ungerminated seeds survived longer flooding, however, for late seedlings appeared in areas which had been covered with several feet of water at about 8° C. for at least 18 days. Flooding, therefore, is definitely a controlling factor in survival of the seedlings of *I. pallida* on the floodplain.

There are of course many other factors, other than those studied here, which undoubtedly affect these plants. This study may be considered as a beginning in the complete ecological life history study of *Impatiens*.

SUMMARY

The purpose of this ecological life history study was to explain the distribution and population density of *Impatiens biflora* and *Impatiens pallida*. Several characters were found which could be used to distinguish the species from each other; among these are the absence of waxy bloom, the fewer number of leaf serrations, the orange flower color, and the presence of ridges on the seeds of *I. biflora*. The geographical distribution of *I. biflora* was found to be more northerly than *I. pallida*, although they overlap over most of their ranges. A distribution map of Minnesota showed *I. biflora* throughout the state and *I. pallida* almost exclusively confined to the southern counties.

I. pallida was found to be characteristic of the floodplain subclimax forest while *I. biflora* was more widespread but apparently confined to habitats with continuous abundant moisture through the summer. *I. biflora* was found to be in considerably denser colonies than *I. pallida*. It was believed that this difference was related to differences in soil moisture requirements of the two species.

Gall insects were observed to have little influence on the vigor of both species.

An experiment showed that lack of aeration had a deleterious effect on the survival of *I. pallida*, but

little or no effect on I. biflora. Adventitious roots formed readily on both aerated and non-aerated cultures of I. biflora, but no adventitious roots formed on I. pallida. It was concluded that the ability to form adventitious roots was an important factor in survival of a plant in a soil lacking in sufficient oxygen.

The ratio of the number of showy flowers to cleistogamous flowers was found to increase over a five-day period, beginning at the time of the appearance of the first showy flower.

The "popping" of the fruit was attributed to the strains produced during development.

The weights of the seeds of both species agree with values obtained by Salisbury for seed weight in relation to habitat.

Field observations and experiments on storage conditions showed that I. pallida requires a period of exposure to winter conditions before the seeds will germinate. During the winter exposure, there was no change in the gross appearance of the seeds.

Measurements of soil temperature around germinating seedlings showed that I. biflora can germinate at a lower temperature than I. pallida.

Survival of I. pallida seedlings after flooding was studied. It was found that 10 days of submergence killed off all I. pallida seedlings, but ungerminated seeds were not affected.

Clusters of seedlings of both species are a striking character of the seedling stage. The cause of the clusters was attributed to the gathering and caching of the seeds by rodents. The mortality rate of seedlings in clusters was found to be very high and was probably due to competition for water.

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