1975

The Comparative Ecology Of Three Riverbank Annuals, Polygonum Lapathifolium L, P Pennsylvanicum L And P Persicaria L

Richard John Staniforth

THE COMPARATIVE ECOLOGY OF THREE RIVERBANK ANNUALS, *POLYGONUM LAPATHIFOLIUM* L., *P. PENSYLVANICUM* L. AND *P. PERSICARIA* L.

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario

March 1975

ABSTRACT

THE COMPARATIVE ECOLOGY OF THREE RIVERBANK ANNUALS, POLYGONUM LAPATHIFOLIUM L., P. PENSYLVANICUM L. AND P. PERSICARIA L.

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In order to survive on gravel banks of rivers, plants must be able to endure special environmental conditions. The gravel banks along the upper stretches of the Thames River, near London, Ontario are submerged for long periods during the autumn, winter and spring; during these seasons plants or seeds tolerate flooding and gravel movements. In the late spring, germinating seeds and seedlings are subjected to rapidly falling soil water tables with the accompanying drying of the porous soils. At this time, short term flooding and gravel movements occur after heavy rains and must be endured by seedlings if they are to survive. In the summer, the plants grow in dry soils with low nutrient status. In this study, the distributions of several common plant species on gravel banks are determined and then each life history phase of such species is examined in a search for adaptations which maximize the chances for survival on gravel banks. The closely related annuals, Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L. are frequent constituents of

the flora of gravel banks along the Thames River. Provincial distribution maps and local surveys show that P. persicaria is a weedy species in Ontario and occurs to a lesser extent on gravel banks; P. lapathifolium is frequent on the low lying and moderately damp parts of gravel banks and occurs throughout the province, whereas P. pensylvanicum is primarily restricted to the drier parts of gravel banks in southern Ontario.

The dispersal of achenes plays a significant role in the colonization of gravel banks from one growing season to the next. Field studies show that achenes are dispersed by hydrochory and by endozoochory. The results of laboratory experiments provide new information concerning floating durations, subsequent achene viability, selective forces on certain achene sizes and dormancy changes. The achenes are produced at a time coincidental with the most efficient utilization of the dispersal agents and they are morphologically adapted to maximize the success of each stage of dispersal (i.e. acceptance, carrying and deposition of the diaspores by the dispersal agents). P. pensylvanicum may be restricted to riverbanks because its large achenes are all destroyed by mastication and, therefore cannot be dispersed by cottontails.

Innate and enforced dormancies are important adaptations for survival on gravel banks where flooding or burial are frequent events in winter. Autumn germination

and the risk of subsequent mortality due to unfavourable weather is prevented by an innate dormancy which is broken only after long periods at low temperatures. Achenes which sink or become deeply buried exhibit an enforced dormancy. Achenes of P. persicaria are rendered inviable when stored in wet gravel bank soils.

On waterlogged soils seedling growth is temporarily arrested. Seedlings of P. lapathifolium are intolerant of burial, a feature not found in the other species. Plants of P. lapathifolium grow largest in soils with a moderate water content, whereas, those of the other species are largest in drier soils.

All three species possess adaptations which could be identified as aids to survival on riverbanks. The loss of viability in achenes of P. persicaria in wet soils and the inability for achenes of P. pensylvanicum to be dispersed by cottontails probably limit the distributions of these species over gravel banks and in other habitats in southern Ontario.

ACKNOWLEDGEMENTS

I should like to thank, most sincerely Dr. P. B. Cavers who supervised this project, for his helpful advice, interest and judgement at all stages of this work.

I am also grateful to Dr. D. A. McLarty and Dr. L. Orlóci for acting as my advisory committee and for their suggestions during the formation of the research proposal and preparation of the thesis.

Fellow graduate students and members of the faculty of the Department of Plant Sciences have offered advice throughout this work and to them I am most grateful. I should like to thank, especially, Dr. R. Gittins, Dr. R. Jancey, Dr. L. Orlóci and Mr. M. Beshir for their assistance with statistical problems.

The greenhouse staff, headed by Mr. J. Johannesen and Mr. P. Thomsen have been most helpful in many ways throughout this project and I should like to thank them all. Mrs. D. Rowley, Mrs. L. McKay and Mr. A. Noon have offered valuable technical assistance during experimentation and reproduction of the results, to them I am also very grateful. I would like to thank Mrs. Stefani Tichbourne for typing the final draft of this thesis.

Thanks are extended to employees of The Upper Thames River Conservation Authority; The Water Resources Unit, Environment Ontario and The London Weather Office, Environment Canada for furnishing me with relevant information concerning

the study area.

Special thanks are due to my wife, Diana for the many hours spent in counting achenes, typing and for her unfailing encouragement throughout the project.

Financial support for this work was provided by a grant from the Canadian National Sportsmen's Show to Dr. P. B. Cavers and also demonstratorships made available by the Department of Plant Sciences at this University.

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CHAPTER I

INTRODUCTION

I.1 Introduction

Riverbank habitats along the Thames River near London (42°59'N 81°14'W), Ontario are subject to extreme seasonal variations in water supply. Plants which inhabit the zone between the high and low water levels are affected by flooding, drought and the consequences of these such as burial, undermining, periodic changes in aeration and nutrient status.

Plant species of habitats where catastrophic events occur frequently must exhibit biological features which enable them to survive environmental change. The timing of each life history phase (i.e. vegetative growth, flower production, pollination, seed development, dormancy, propagule dispersal, germination and seedling establishment) must correlate with the most suitable set of periodically or seasonally occurring environmental conditions. The phenotype must exhibit ecological adaptations to the contemporary environmental conditions during each of these life history phases by genetic expression, plasticity or both. The mode of pollination and numbers of propagules produced must allow the maintenance of a genetically and numerically viable population.

Many riverbank plants are annuals and as such need to re-colonize the habitats each year. The seeds and fruits

are extremely important in this function as not only are they the sole overwintering propagules but also the dispersive phase of the life history. The seeds and fruits of annual plants growing in changeable habitats frequently show many morphological and physiological adaptations for efficient overwinter survival and efficient dispersal.

I.2 Purpose

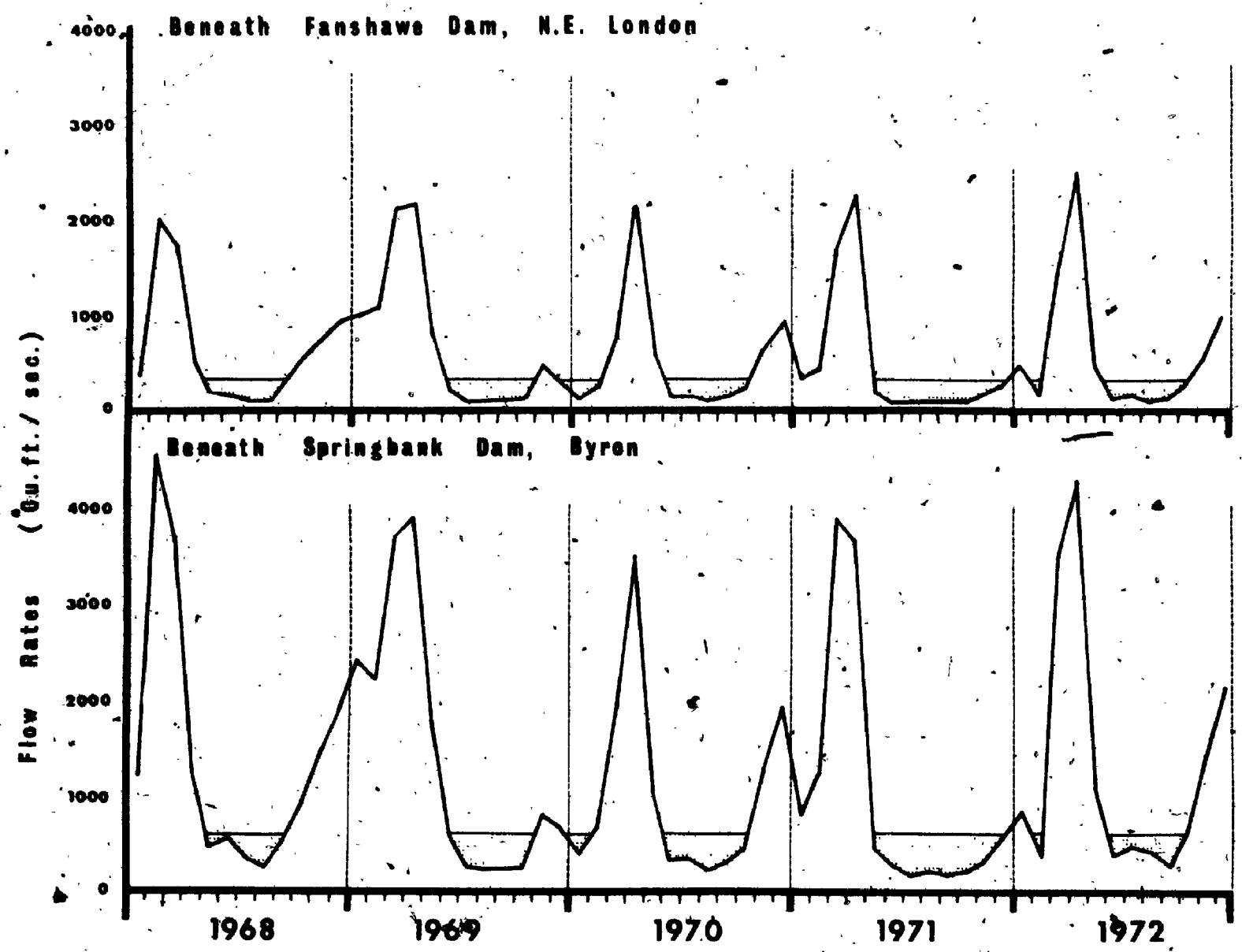
The purpose of this thesis is to examine biological features which allow different species of the genus Polygonum L. to occur frequently on gravel banks.

The study is largely autecological; this permits observations to be investigated with experiments of a manageable size. However, discussions of habitats in which experiments were undertaken and in which the plants occur would be incomplete without mentioning accompanying species or plant associations. For this reason Chapter II and sections of other chapters are of a more synecological nature.

The study is comparative, concerning three closely related common species which occur in the same habitat. An emphasis has been placed on examination of the process of dispersal. This aspect of a plant's life history is very important to colonizing species and one which has been largely ignored in experimental studies.

I.3 Choice of species

The species chosen for this study were Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L.


Beneath Fanshawe Dam, N.E. London
Beneath Springbank Dam, Byron
Flow Rates (cu.ft./sec.)
4000
3000
2000
1000
0
1968
1969
1970
1971
1972

the early pioneer species (e.g. the annual plants of the embryo dunes of a sand dune sere.).

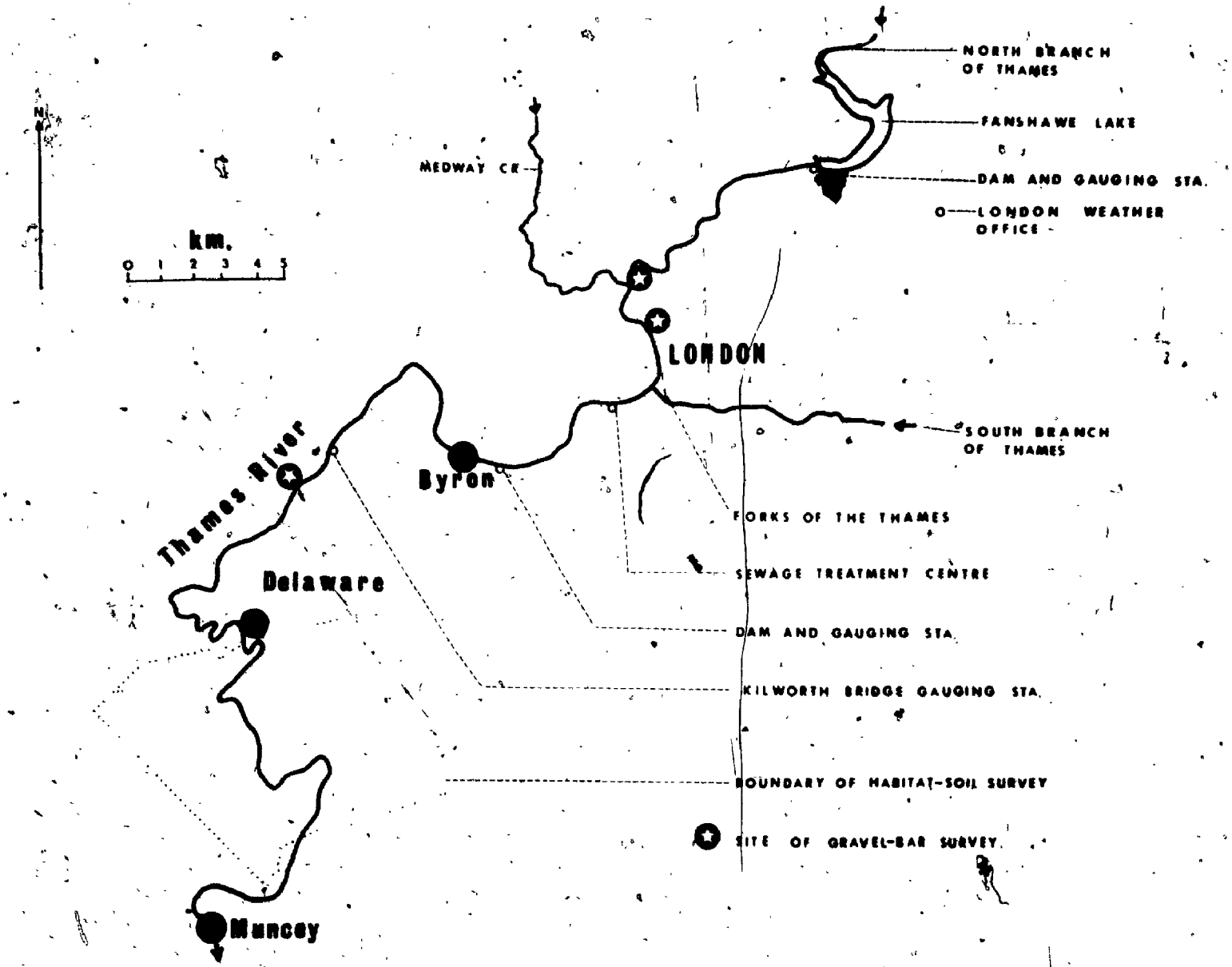
7. A comparison is possible between P. pensylvanicum, a native species; P. persicaria, an alien species and P. lapathifolium, a species which is native but has had its population augmented by accidentally introduced stock (Gleason 1963).

I.4 Delimitation of the study area

It was necessary to define an area to which surveys, seed collections and plant collections would be limited. The area chosen was restricted to the banks of the North Branch of the Thames River from Fanshawe Dam (43°80'N 81°13'W) to its junction with the South Branch and then southwest to the village of Muncey (43°69'N 81°15'W). The river and its margins proved suitable for this study, except for one survey, when the study area was extended away from the immediate banks of the Thames (Fig. I.1). This area offered the following advantages:

1. It is easily accessible.
2. Gravel bars are frequent.
3. The study species are abundant.
4. The water-shed includes a wide range of soil types.
5. Much environmental information is available from government agencies, such as the Upper Thames River Conservation Authority (with stations at Byron and Fanshawe Dam) and the Lower Thames Valley Conservation

FIG. 1.1 FEATURES OF THE STUDY AREA.


N
km.
0 1 2 3 4 5
NORTH BRANCH OF THAMES
FANSHAWE LAKE
DAM AND GAUGING STA.
LONDON WEATHER OFFICE
MEDWAY CR.
LONDON
SOUTH BRANCH OF THAMES
Thames River
Byron
FORKS OF THE THAMES
SEWAGE TREATMENT CENTRE
Delaware
DAM AND GAUGING STA.
KILWORTH BRIDGE GAUGING STA.
BOUNDARY OF HABITAT-SOIL SURVEY
SITE OF GRAVEL-BAR SURVEY.
Muncey

Authority. The former supplied data on river flow and suspended solid particles. The Water Qualities Branch, Environment Canada, also with stations at Byron and Fanshawe Dam, provided quantitative information concerning water temperature, pH, pollution and nutrient status of the river. Finally the London Weather Office (Atmospheric Environment Service, Environment Canada) made available climatic data gathered at London's Crumlin Airport.

I.5 The riparian habitat

Determining how plant species survive in harsh riparian environments requires a detailed knowledge of the variables affecting all of the life-history phases of the plants.

I.5.1 The climate

Climate influences plants directly; or indirectly by modifying their environment. The following discussion refers to the study area.

Precipitation averages 94 cm. per year occurring as snow (between the approximate dates of November 22nd and March 30th) and rain (Brown, McKay and Chapman 1968). Monthly totals vary greatly and irregularly; especially in the months May to September; the growing season of many plant species. Dry and wet periods severely affect soil water contents in riparian habitats. Extended dry periods occur more frequently than wet periods during the growing

season. Table I.2 shows the number and duration of dry and wet periods during the growing seasons in which the study was undertaken. A "dry period" is defined as the number of consecutive days with less than 0.25 cm. of precipitation. A "wet period" is defined as the number of consecutive days with more than 0.025 cm. of precipitation. These definitions of dry and wet periods are used by Brown, McKay and Chapman (1968). 1968 was unusually wet and 1971 unusually dry, both during the growing seasons (May to September) and the entire years (see Tables I.1, I.2 and Fig. I.2).

Air temperature has many influences on plants of riparian communities. The mean daily temperature is below 0°C from the middle of November to the middle of March (see Fig. I.2). The growing season for many perennial crops (a period when the mean daily temperature is above 5.6°C) lasts from mid-April to mid-October. However, the last frost in the spring and first frost in autumn (given in Table I.1) shorten the growing season for frost sensitive species. Plant growth is dependent on the length of the growing season and on the amount of heat available through its duration. The latter is usually defined as the number of degrees the daily mean temperature exceeds 42°F and can be totalled for the year as degree-day heat units. A comparison of the length (measured in frost free days) and quality (degree-day heat units; Brown, McKay and Chapman 1968) of the growing seasons for the five year study period is given in Table I.1.

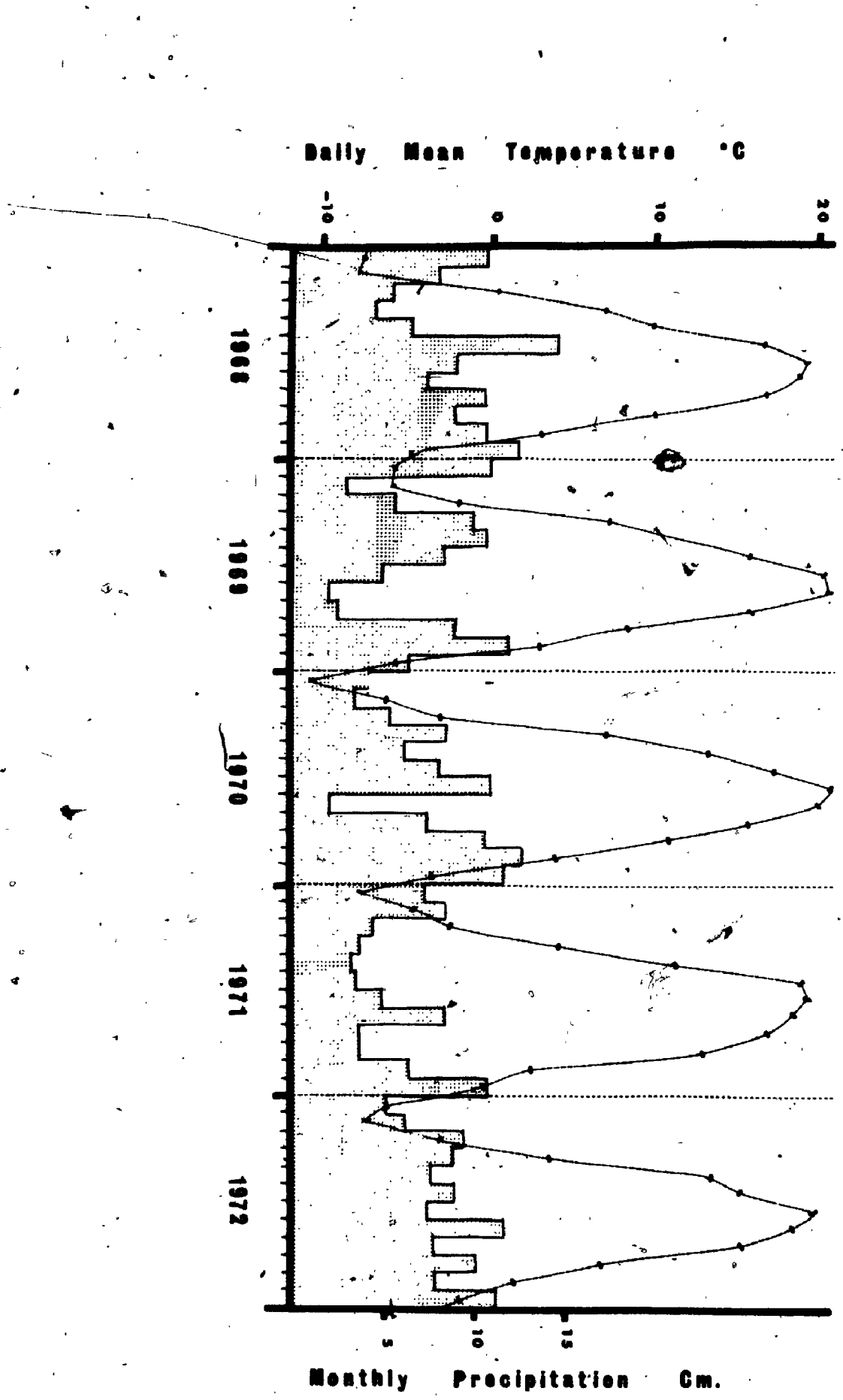
Table I.1- Summary of climatic data for the London area.

Year	1968	1969	1970	1971	1972	30 yr. mean (1931-1960)
Precipitation (cm.)						
-per year	110.7	87.1	89.1	61.3	105.9	94.0
-May to September	54.1	29.1	33.8	24.2	44.4	39.4
Daily Mean Temperature (°C)						
-annual mean	6.9	7.0	7.1	6.1	6.4	7.8
-January mean	-7.9	-5.9	-10.9	-8.0	-5.9	-5.0
-July mean	19.3	20.4	20.7	19.4	19.9	20.8
Frosts						
-last spring frost	May 7	May 26	May 7	May 13	June 11	May 13
-first autumn frost	Oct 30	Sept 29	Oct 11	Oct 7	Oct 9	Oct 5
-consecutive frost free days	176	126	157	147	119	145
Degree days above 42°F per year	3542	3582	3867	3763	3283	3600

Table I.2 Frequencies of dry and wet periods in London, Ontario during the months May to September for five consecutive years of study.

Year	Consecutive dry days				Consecutive wet days	
	7-13	14-20	21-27	>28	5-6	>7
1968	6	0	0	0	2	0
1969	5	0	0	1 (42 days)	1	1 (8 days)
1970	2	1	1	0	2	0
1971	5	2	1	0	1	0
1972	5	1	0	0	2	0

FIG. I.2 TEMPERATURE AND PRECIPITATION RECORDED AT THE LONDON WEATHER OFFICE.


Daily Mean Temperature °C
-10
0
10
20
1968
1969
1970
1971
1972
5
10
15
Monthly Precipitation Cm.

Lubke (1968) suggested that wind is not an important factor along the Thames River because the water course is protected by the riverside woodland, the banks themselves and the valley sides. This conclusion is substantiated by the rarity of erosion, deposition, plant damage and propagule dispersal by wind. The dessication of the exposed substrate in summer and autumn by light breezes is unlikely, as the air has a very high humidity level during these periods.

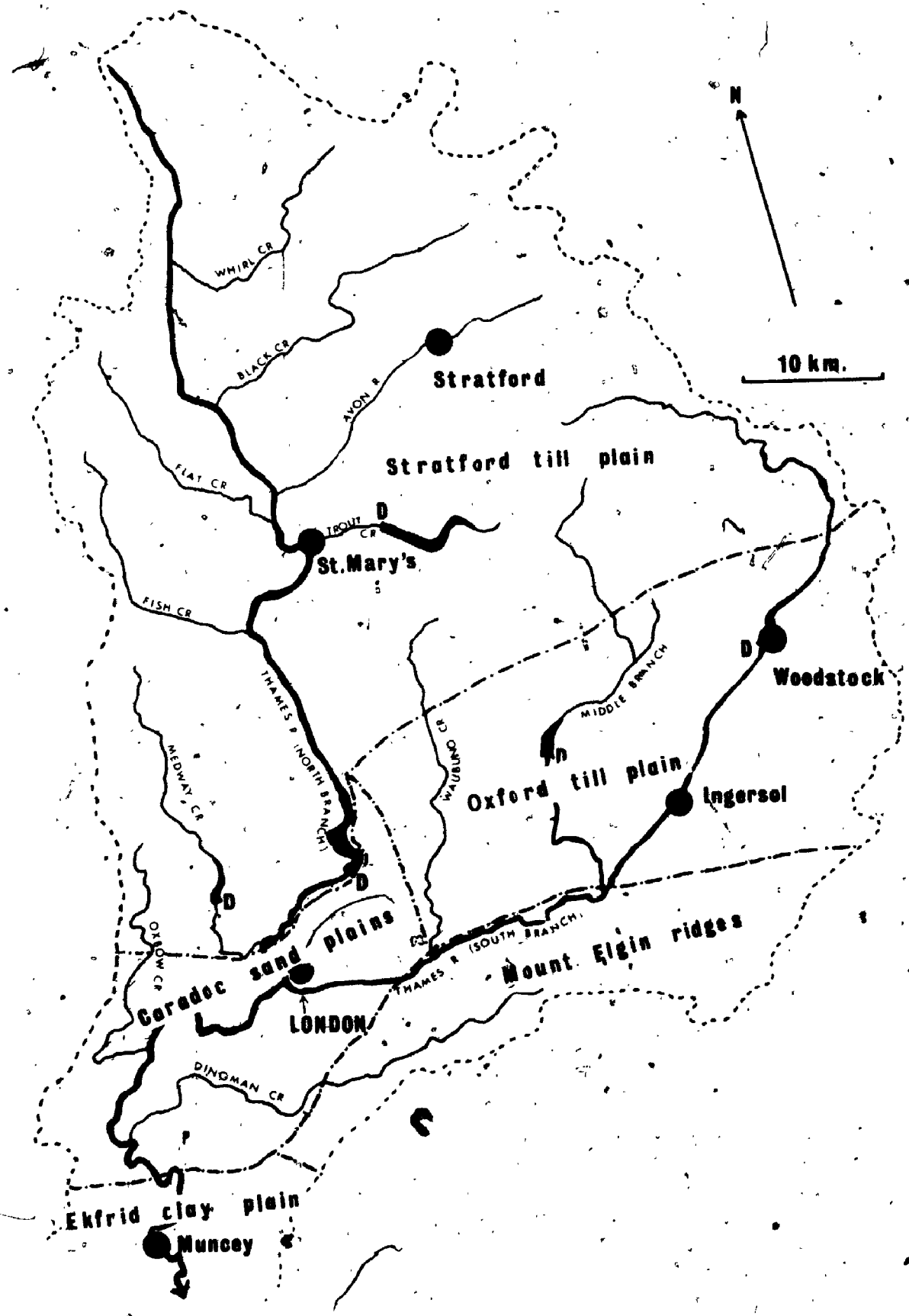
An adequate light intensity is essential for plant growth and the duration or quality is a trigger for flower initiation or germination in some plant species. Illumination, directly onto the plants and by reflection from the light coloured substrate may be so intense as to be damaging to the plant tissues. Nozzolillo (pers. comm.) has suggested that the red anthocyanidin pigment in the stems of Polygonum spp. may be protective.

I.5.2 The hydrology of the watershed

The Thames watershed above the village of Muncey is illustrated in Figure I.3. The entire watershed covers an area of 2,252 square miles originating in the swamps of Perth and Oxford Counties (Anon., 1952, Anon., 1966). The river's total length is 190 miles, with the mouth on the eastern shore of Lake St. Clair. The North Branch meets the South Branch at the Forks of the Thames in London. Many tributary streams enter the North Branch, the major ones being Medway Creek, Trout Creek and the Avon River. The

FIG. I.3 PHYSIOGRAPHY OF THE THAMES WATERSHED ABOVE MUNCEY.

OXFORD TILL PLAIN	- calc. loams and boulders
STRATFORD TILL PLAIN	- clay plain with gravelly vallies
MT. ELGIN RIDGES	- clay silt morraines with gravel sand, silt vallies
CARADOC SAND PLAINS	- clay plains with deposits of silt, sand and gravel
EKFRID CLAY PLAIN	- alternate layers of clay, sand and gravel
D	- dam


N
10 km.
WHIRL CR
BLACK CR
AVON R
Stratford
Stratford till plain
FLAT CR
TROUT CR
St.Mary's
FISH CR
THAMES R (NORTH BRANCH)
MEDWAY CR
WAUBUNO CR
MIDDLE BRANCH
Woodstock
Oxford till plain
Ingersol
OXBOW CR
Caradoc sand plains
THAMES R (SOUTH BRANCH)
Mount Elgin ridges
LONDON
DINGMAN CR
Ekfrid clay plain
Muncey

South Branch is joined by fewer tributaries, the notable ones being the Middle Branch (the junction of the South and Middle Branches was originally known as the Forks of the Thames) and Waubuno Creek.

The quantity and flow rate of water in the Thames River affects habitat exposure, erosion, sediment transportation, deposition and nutrient content of the substrate. The quantity and flow rates are determined by many factors; precipitation, run-off, dams, evaporation, soil absorption, man and plants, drainage pattern, rate of descent and occurrence of obstacles in the river course. Figure I.4 illustrates the seasonal variation in flow rate measured in cubic feet per second based on data obtained from the Upper Thames River Conservation Authority (U.T.R.C.A.). Approximate water depth can be estimated from the flow rate by equating fifty cubic feet per second with one foot in depth (Mr. L. Johnson, pers. comm.).

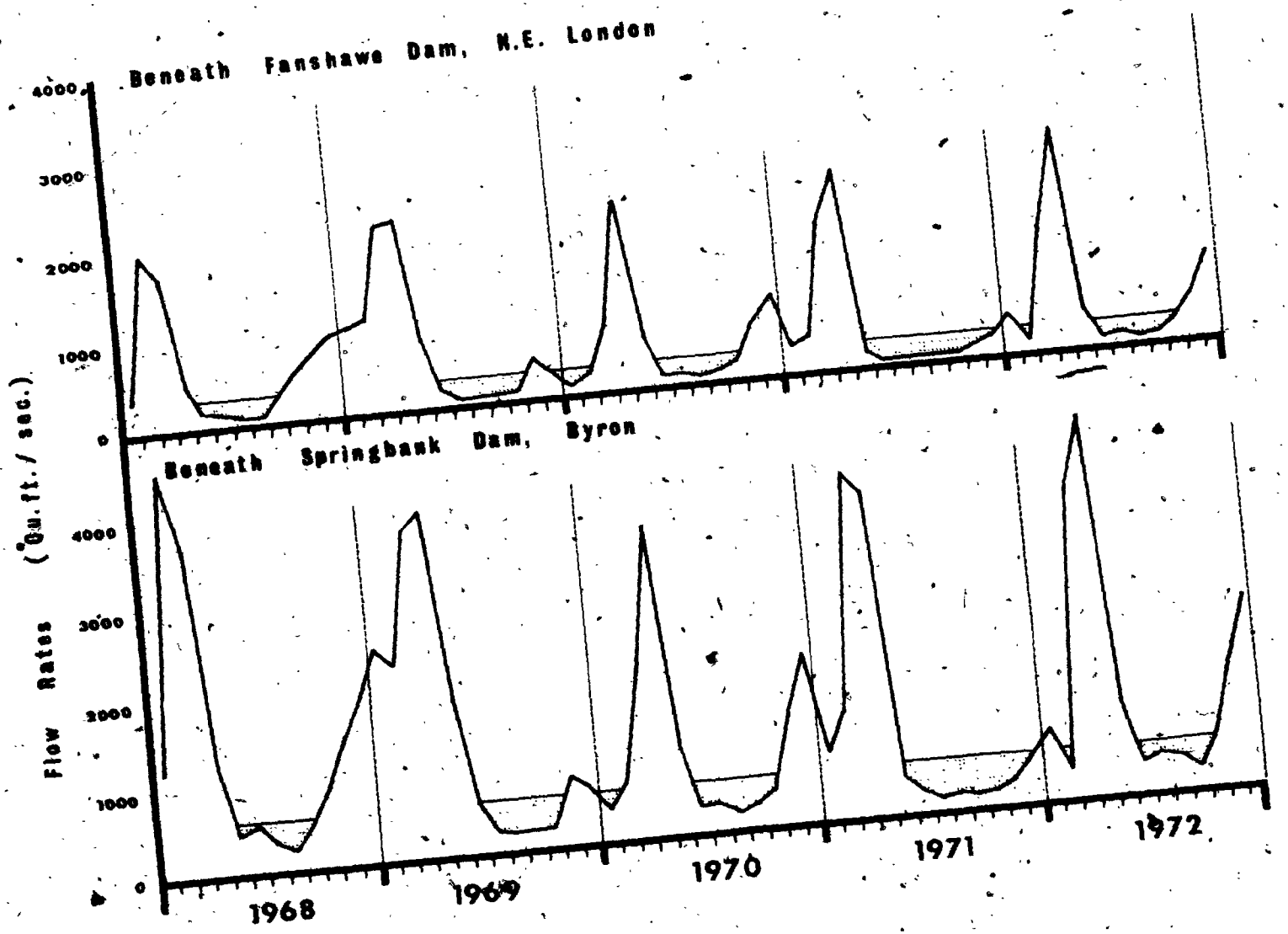
During February and March the rate of flow increases greatly as the snow cover melts causing high run-off from the frozen soils of the watershed. Heavy rain storms at this time can augment the high run-off volume. The three gravel bars which were studied during 1970 (Chapter II) may be flooded by up to eight feet of water at this time (see Plates 1-3). As the melt water decreases and dry periods become more frequent the bars become more exposed. This exposure commences in mid-April and reaches a maximum in late August when the flow rate is minimal. The U.T.R.C.A.

Table I.5 A summary of seasonal changes in the riparian habitat along the Thames River, Southern Ontario.

Month	J	F	M	A	M	J	J	A	S	O	N	D
Bar exposure	← flooded →			← exposed →						← flooded →		
Flow rate	← high →			← low →						← high →		
Erosion/deposition	← high →			← low →						← high →		
Relative levels of dissolved nutrients in river water	Ammonium and chloride ions fluctuate irregularly throughout the year.											
	Dissolved Oxygen, Soluble Phosphorus, Soluble Nitrates: high →			← low →						← high →		
Mean numbers of degree day heat units per month	← nil →			← inc. →		max.	← dec. →			← nil →		
Mean dates for important temperatures				← frost free days →								
				Daily mean temp. 6°C →								
				← 0°C →								
Probability of dry and wet periods				<High for dry periods>								
				<Low for wet periods>								

FIG. 1.4 RIVER FLOW RATES AND APPROXIMATE PERIODS OF GRAVEL BAR EXPOSURE AT TWO PLACES ON THE THAMES RIVER.

(Shading shows approximate duration of bar exposure.)


Beneath Fanshawe Dam, N.E. London
Beneath Springbank Dam, Byron
Flow Rates (Cu. ft. / sec.)
4000
3000
2000
1000
0
1968
1969
1970
1971
1972

maintains a minimum flow rate of 150 cubic feet per second by dam operations (Mr. L. Johnson, pers. comm.). This ensures that effluent from the Greenway Pollution Control Centre in London is diluted by at least three parts of water to one part of effluent. In order to meet this demand, excess water is conserved behind several dams during the summer months. During the summer, soil water retention prevents an increase in the flow rates of tributary streams after precipitation. In the autumn, a low water level is retained behind the dams and this practice ensures that they are capable of holding and gradually releasing the spring run-off. This results in fluctuating autumn levels and flow rates.

Water quality and quantity are important to this study for two reasons. Firstly, due to the porous nature of gravel bar and riverbank soils, the river water is often in direct contact with the roots of plants growing on them. Nutrients in the river water, therefore, have a direct influence on the plants. Secondly, as indicated by turbidity measurements, the extent of erosion may be severe at different times of the year.

Data concerning water temperature, amounts of dissolved oxygen, suspended solids, soluble phosphorus compounds, soluble ammonium compounds, nitrate ions, chloride ions and pH, collected by the Water Qualities Branch, are summarized in Table I.3. Nutrient status is high when there is much run-off from the watershed. The nutrient concentrations are augmented

Table I.3 Water quality data from the Thames River (monthly means, 1968-1971). The first value of each pair was recorded at Fanshawe Dam (F) the second at Byron (B) downstream from London. A dash (-) indicates no data recorded.

Month		J	F	M	A	M	J	J	A	S	O	N	D
Water temp. C.	F	0	0	1	8	14	19	25	24	20	13	6	1
	B	0	1	2	12	15	20	24	23	18	13	8	2
Dissolved oxygen Mg./L.	F	11	8	12	9	9	9	9	6	7	9	9	-
	B	10	10	11	11	9	9	8	8	7	8	8	10
Total solids Mg./L.	F	387	340	360	288	319	287	298	284	270	327	353	339
	B	411	396	378	373	389	378	387	394	403	406	427	417
Soluble phosphorus Mg./L.	F	.08	.11	.08	.06	.04	.02	.03	.03	.05	.03	.04	.07
	B	.21	.23	.20	.12	.14	.24	.45	.31	.42	.47	.35	.24
Ammonia as nitrogen Mg./L.	F	.19	.35	.25	.14	.14	.16	.24	.12	.28	.16	.19	.41
	B	.06	.56	.45	.16	.26	.40	.29	.35	.44	.47	.63	.46
Nitrate as nitrogen Mg./L.	F	3.5	2.7	3.5	2.3	2.1	0.8	0.8	0.2	0.2	0.8	2.7	1.5
	B	3.2	3.5	3.4	2.8	2.0	1.3	1.4	1.3	1.2	1.6	2.1	3.4
Chloride Mg./L.	F	15	13	16	11	13	15	17	19	16	16	18	21
	B	27	27	24	20	22	33	36	39	39	35	32	34
pH.	F	8.3	8.2	8.1	8.2	8.1	8.2	-	8.1	8.1	-	8.4	8.3
	B	8.3	-	8.2	8.4	8.2	8.2	8.2	8.3	8.0	-	8.1	8.1

by effluent from the pollution control centres and from storm sewer outlets. Summer evaporation may concentrate nutrients on the gravel and sand surfaces. Water temperature fluctuates yearly by about 25°C. The higher summer temperatures are associated with reductions in dissolved oxygen. The average pH value is just over 8.0. This can be expected considering the basic nature of the soils and bedrock in the watershed.

I.5.3 Soils

The gravels and other sediments of the Thames River are derived from Devonian limestone and dolomitic bedrock and from the glacial soils deposited at the recession of the Wisconsin glaciers about twelve thousand years ago (Chapman and Putnam 1966). Sediments of the latter origin have been washed into the river drainage system from the watershed. Such sediments were deposited as till plains, eskers, drumlins and other glacial formations (Fig. I.3). More recently, near Lambeth (about 8 or 10 thousand years ago), the sediments formed two gravel beaches on the shores of the former Lake Whittlesey, a precursor of Lake Erie.

The soils of bars and riverbanks are classified by soil surveyers as lithosols. Lithosols are characteristically stony and show little horizon formation. Occasionally the river course may expose gley soils or podsolic soils at its banks but because the bed of the Thames River has fluctuated since the recession of the Wisconsin Glaciers, the development of zonal soils has effectively been retarded.

Leopold, Wolman and Miller (1964) describe some features of bars and riffles (submerged bars) of which the following are relevant to this study.

1. Bars and riffles are comprised of coarser fragments than the beds of adjacent pools.
2. Experiments with painted pebbles have shown that while bars move extremely slowly as units, their component particles may appear on the next bar one year later. This movement of the coarse components is of a creeping nature and occurs during small rapid increases in flow rate rather than sudden movements during floods.
3. Simple deposition of particles would result in larger components being deposited on the upstream side of the bar and smaller particles on the downstream side.

Gorchakovskii and Peshkova (1970) and Hill and Hanley (1914) have described this horizontal grading of particle sizes from the Middle Ural River and sea beaches respectively. Observations of the Thames River by the author, have indicated a more complex situation with much mixing of particle sizes. The causes of this mixing include:

(a) Convoluted and dendritic drainage patterns within the exposed bars.

(b) Accumulation of leaf litter and other debris amongst the larger pebbles resulting in local deposition of finer particles.

(c) Continual movement of the bar.

(d) Small differences in flow rate and current direction (e.g. eddies) within the region of deposition.

Kopecky (1965) found that points of erosion and deposition are not constant but shift with time. He also emphasized the role of vegetation in influencing current speed and direction, erosion and deposition and in stabilisation of the banks.

Soil data for bars on the Thames River was gathered during surveys in August and September 1971 (see Table I.4 and Chapter II). Particles 0.5 to 2.0 mm. and 70 to 250 mm. in diameter were the most abundant on a dry weight basis. The pH values of 7.5 to 8.0 indicated base rich conditions reflecting the high carbonate content of the particles. Potassium, phosphate, nitrate, ammonium, sulphate and chloride levels were in the low to very low range. Occasional samples showed very localized high levels of nitrates, ammonium compounds and phosphates. The water content of the soils varied from complete saturation to a very low percentage in mid-summer. As the water level dropped in early summer new areas became exposed, while previously exposed areas became dryer.

Lubke (1968) has shown that the highly reflective gravel surfaces have temperatures which exceed the air temperature by several degrees on sunny days. However, poor heat conduction by the rocky particles means that subsurface temperatures are often several degrees lower than the corresponding air temperatures.

Table I.4 Soil data from gravel bars on the Thames River in London, Ontario. Each value is the mean of 60 samples. Chemical properties were determined by a Helige-Truog Soil Combination Kit and physical properties are given as percentages by dry weight. The sampling method and soil analyses are described in Chapter II, the location of the bars is shown in Fig. I.1.

a) Chemical properties

pH	8.0	NO_3^-	low
PO_4^{--}	v.low	NH_4^+	low
K^+	low	SO_4^{--}	v.low
Ca^{++}	v.high	Cl^-	v.low

b) Physical properties

Particles (mm.)	%	Particles (mm.)	%
<0.053	1.57	2.00- 35.00	8.08
0.05-0.11	1.38	35.00- 70.00	12.59
0.11-0.50	15.93	70.00-250.00	21.11
0.50-2.00	25.82	>250.00	6.84

c) Water 7.43%

I.6 The environmental seasons of the riverbanks and bars, life histories of annual plants and suggested experiments

The preceding discussion of the riparian environment deals with changes and qualities of individual environmental factors. These factors are chronologically superimposed such that "seasons" can be described which may or may not be favourable for the growth of plants or to certain phases in plant life-histories. These "seasons" vary from year to year in their time of commencement and duration. A summary of seasonal environmental changes is presented in Table I.5 for an "average" year, based on data previously described.

Of the eight life history phases listed at the beginning of this chapter, four were thought to be important for the purposes of the study (see section I.1). These were: achene dormancy, propagule dispersal, germination and seedling establishment. Plants in each of these phases are relatively sensitive to harsh environmental conditions compared with plants which are more mature. Drought is the most severe factor for older plants and they are well adapted for survival by means of their deep and extensive root systems.

The properties of microhabitats, macrohabitats and distributions of each species are considered in Chapter II. Adaptations aiding propagule dispersal are examined in Chapters III and IV. Achene dormancy and germination are treated together in Chapter V. Seedling establishment under various conditions is examined in Chapter VI.

Table I.5 A summary of seasonal changes in the riparian habitat along the Thames River, Southern Ontario.

Month	J	F	M	A	M	J	J	A	S	O	N	D
Bar exposure	← flooded →			← exposed →						← flooded →		
Flow rate	← high →			← low →						← high →		
Erosion/deposition	← high →			← low →						← high →		
Relative levels of dissolved nutrients in river water	Ammonium and chloride ions fluctuate irregularly throughout the year.											
Dissolved Oxygen, Soluble Phosphorus, Soluble Nitrates	high →			← low →						← high →		
Mean numbers of degree day heat units per month	← nil →			← inc. →		max	← dec. →			← nil →		
Mean dates for important temperatures				← frost free days →								
				Daily mean temp.								
				← 6°C →								
				← 0°C →								
Probability of dry and wet periods				< High for dry periods >								
				< Low for wet periods >								

CHAPTER II

DISTRIBUTION

II.1 Introduction

Distribution data for Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L. were examined at various scales of magnitude for several reasons relevant to this thesis:

1. They show the extent to which each species is associated with gravel banks and with other habitats. A species which commonly occupies gravel banks is probably better adapted to this habitat than a species only occasionally found on gravel banks and more usually found elsewhere.
2. Knowledge of habitats with which the species are associated is an essential prerequisite before one can commence experimental studies on the various life history phases. It was necessary to choose relevant environmental factors and determine relevant values for these factors before a study of dispersal, germination and establishment could be undertaken.
3. Dispersal, germination and establishment experiments conducted in the laboratory or greenhouse provide some information concerning factors which limit the distribution of a species. The results of such experiments can be verified only by means of field surveys.

Large scale data on distributions are important as they show discontinuity on a world-wide or continent-wide

basis. Any such associations of species with major vegetation types or areas of intensive agriculture become apparent after drawing such distribution maps. It is also informative to know if a species is on the edge of its distribution in a certain locality, for under such circumstances it may be restricted to very few of the habitats with which it is normally associated. Local habitat and microhabitat surveys are more useful than large scale surveys as they provide more precise and detailed data. For this season Survey IV is described in considerable detail.

Forman (1964) has suggested that distribution data must be used with caution. There are three main reasons for this:

a) The absence of a species in a given area may reflect either a hostile environment or the absence of propagules.

b) Individuals are not necessarily found continuously throughout the range of the species.

c) The identification of limiting factors is difficult. The combined effect of two or more variables may be very different to the effects of the same variables taken individually. These shortcomings can be compensated for by experimentation and by the examination of distributions at different scales.

In this chapter, four surveys are described which were undertaken to examine and compare the distributions of three species of Polygonum on four different scales. These

were:

Survey I World distribution.

Survey II Ontario distribution.

Survey III Distribution amongst various soil types and land uses near London, Ontario.

Survey IV Distribution within gravel banks.

II.2 Taxonomic status of materials

No attempt was made to identify the subspecific taxa of the three species. P. petecticale (Stokes) Druce, P. scabrum Moench., P. nodosum L. and P. tomentosum have been treated as autogamous strains within the species P. lapathifolium (Timson 1963 and see Appendix I).

II.2.1 Survey I. World distribution

Floras and species lists for specific countries and geographical areas were examined for information relating to regional distributions of each of the three species. These data were compiled and presented in map form in Figures II.1-3. The references are listed in Appendix II.1 (a and b).

II.2.2 Survey II. Ontario distributions

The distribution of each species in Ontario was plotted by using data from herbarium specimens (Figures II.4-6). The herbaria (listed in Table II.1) were visited between August 1971 and February 1973. All specimens were scrutinized to ensure that they had been correctly identified (according to Gleason and Cronquist 1963).

FIG. II.1 WORLD DISTRIBUTION OF POLYGONUM LAPATHIFOLIUM.

Arrows indicate isolated records of occurrence.

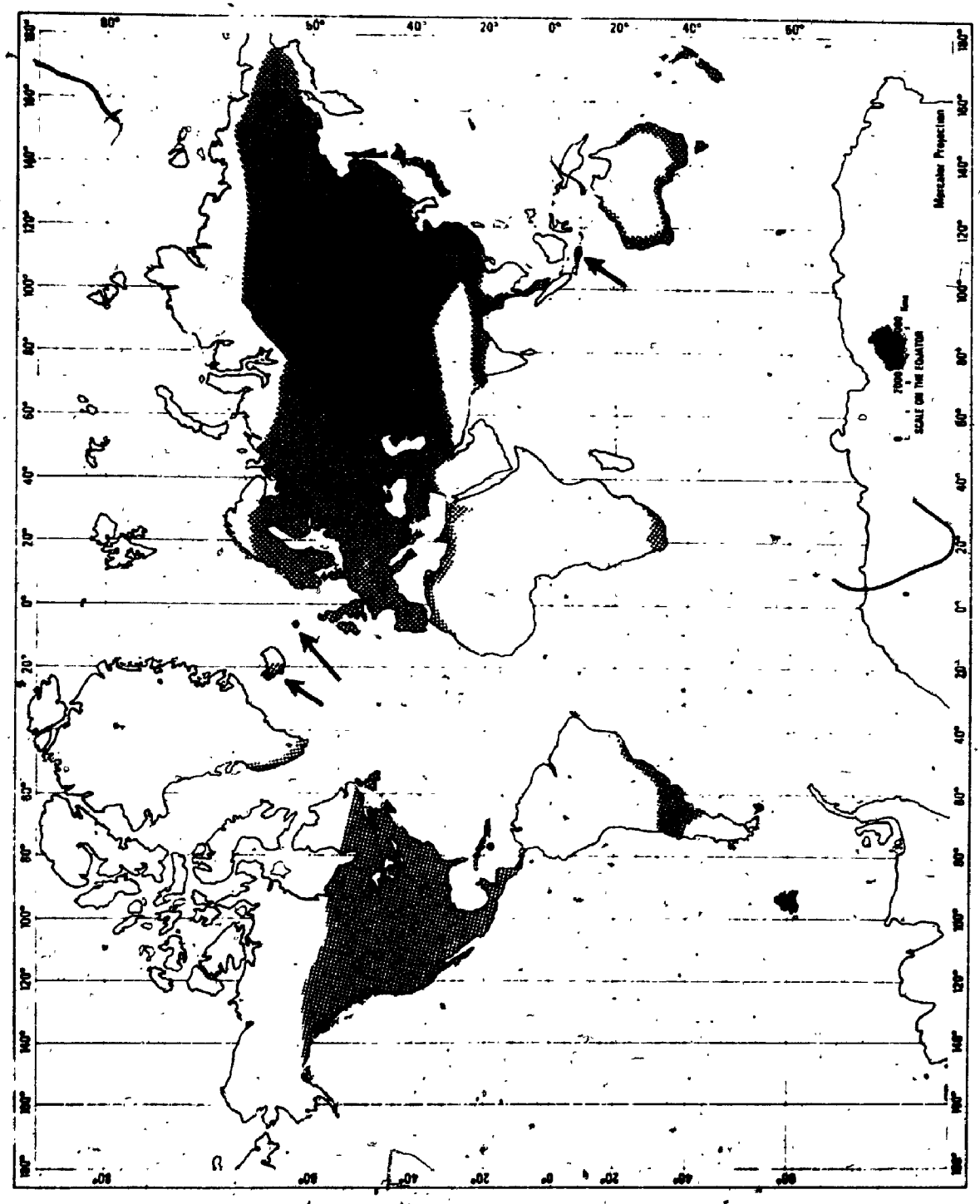

Mercator Projection
SCALE ON THE EQUATOR

FIG. II.2 WORLD DISTRIBUTION OF POLYGONUM PENSYLVANICUM.

Arrows indicate isolated records of occurrence.

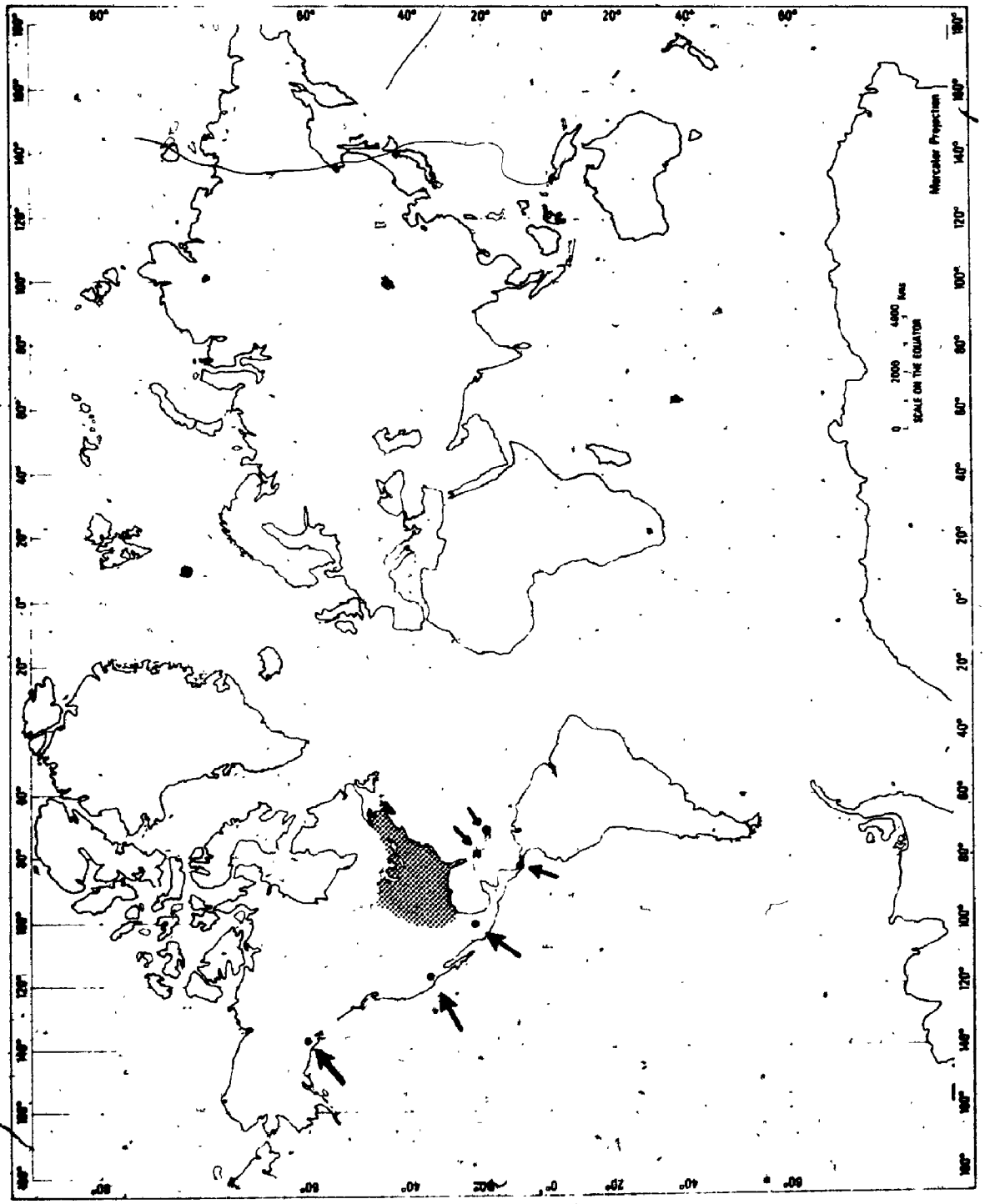

Mercator Projection
SCALE ON THE EQUATOR

FIG. II.3 WORLD DISTRIBUTION OF POLYGONUM PERSICARIA.

Arrows indicate isolated records of occurrence.

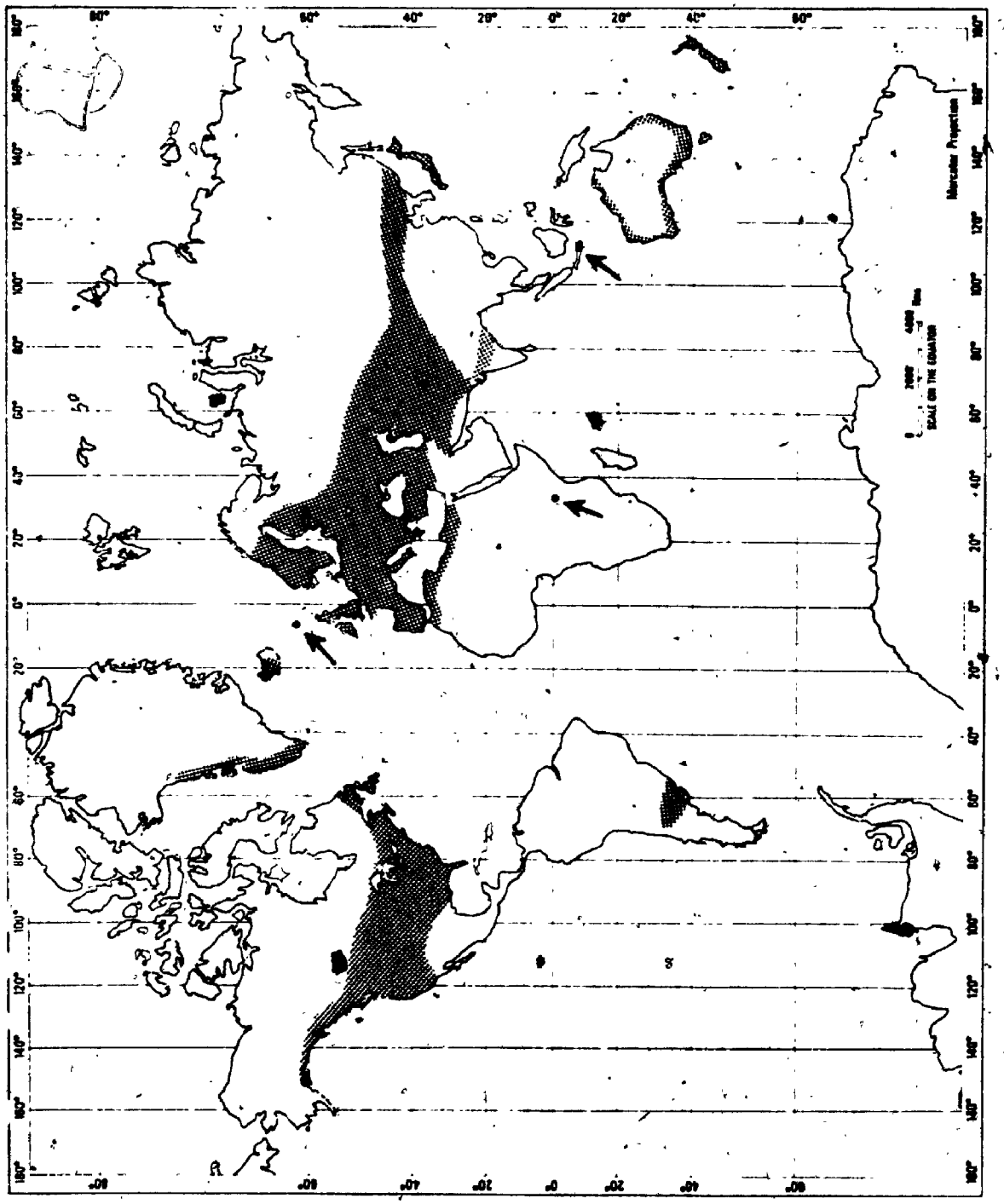

Mercator Projection
SCALE ON THE EQUATOR

FIG. II.4 ONTARIO DISTRIBUTION OF POLYGONUM LAPATHIFOLIUM.

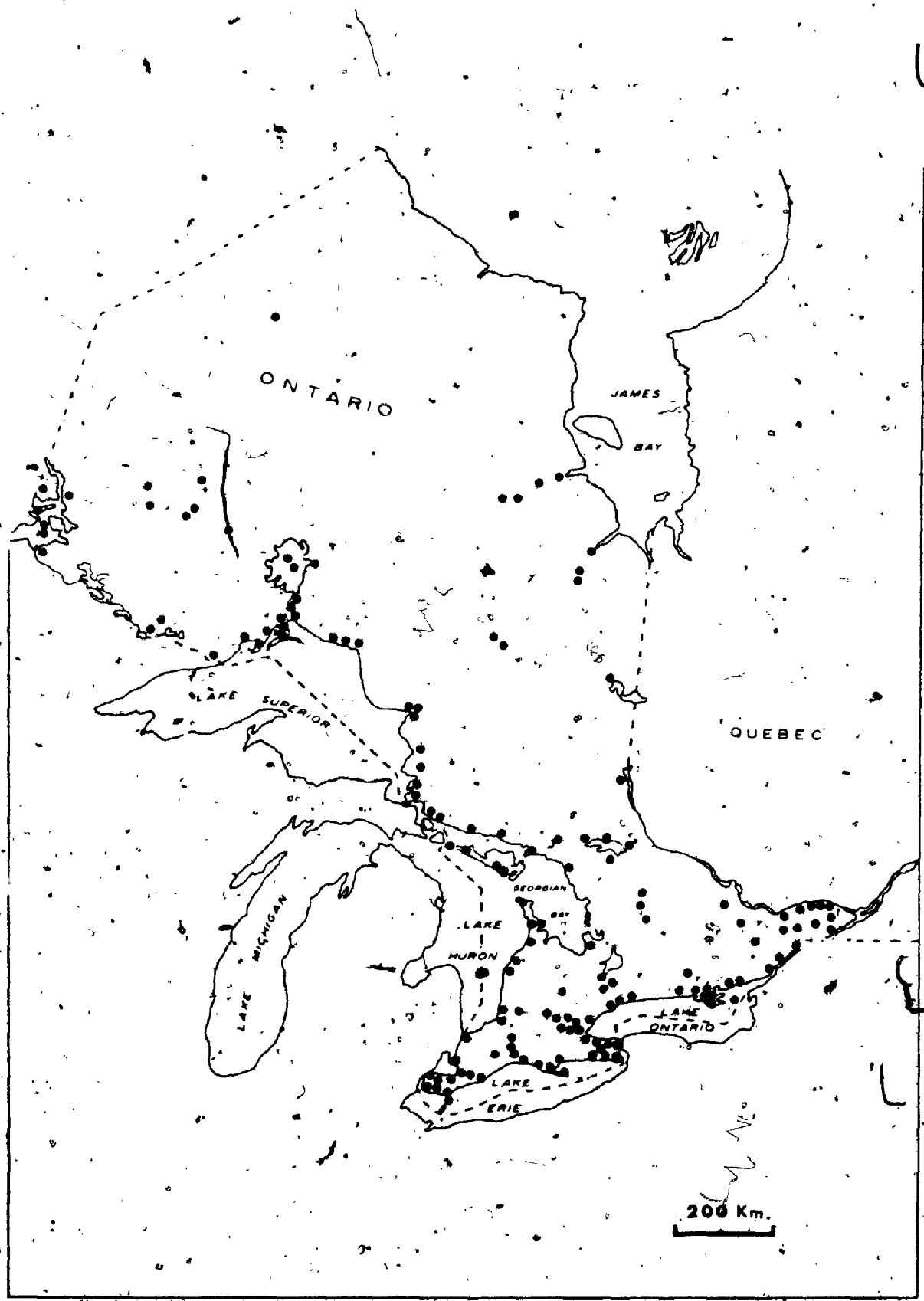

ONTARIO
JAMES
BAY
QUEBEC
LAKE SUPERIOR
LAKE MICHIGAN
GEORGIAN
BAY
LAKE
HURON
LAKE
ONTARIO
LAKE
ERIE
200 Km.

FIG. II.5 ONTARIO DISTRIBUTION OF POLYGONUM PENSYLVANICUM.

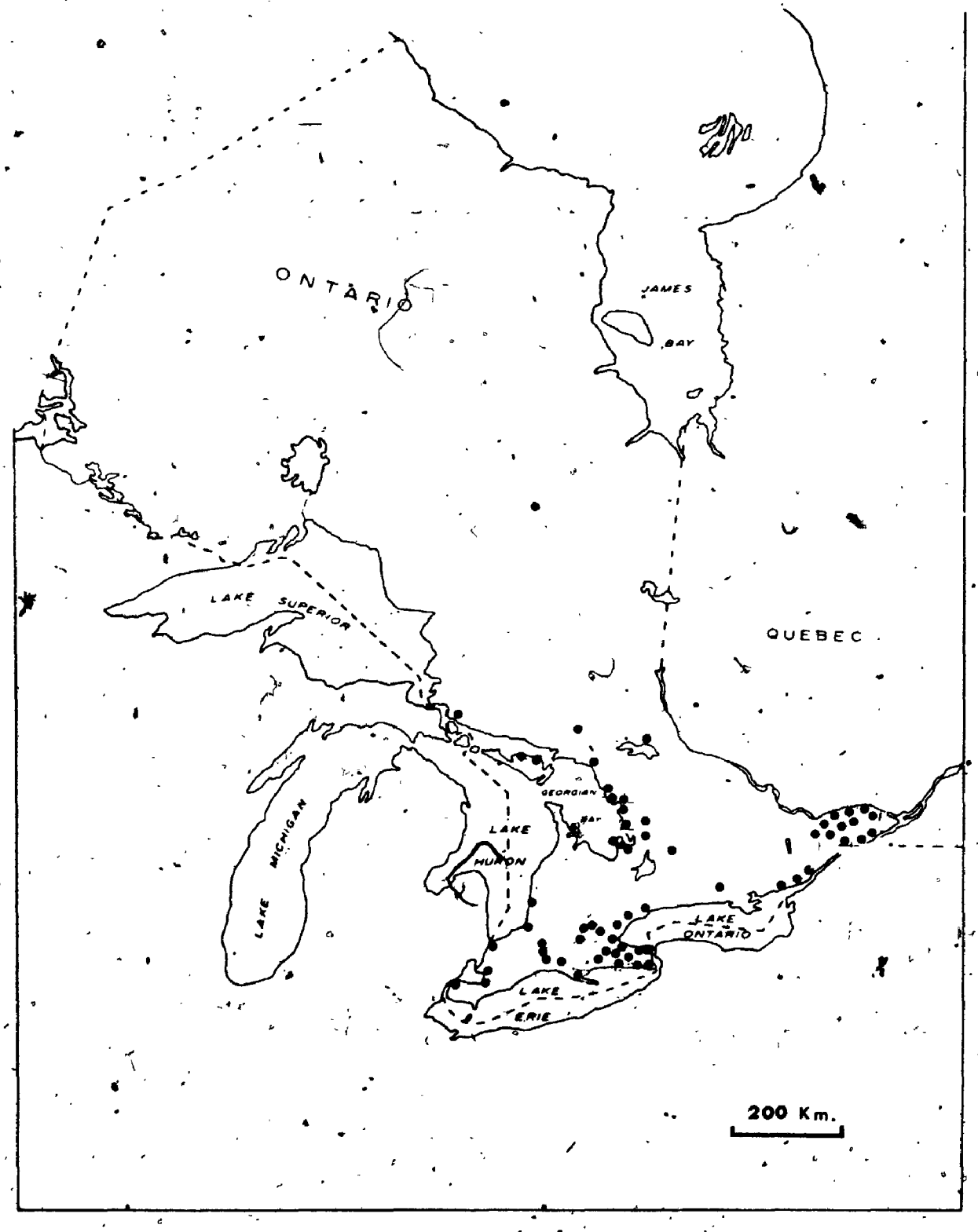

ONTARIO
JAMES
BAY
LAKE SUPERIOR
QUEBEC
GEORGIAN
BAY
LAKE
MICHIGAN
LAKE
HURON
LAKE
ONTARIO
LAKE
ERIE
200 Km.

FIG. II.6 ONTARIO DISTRIBUTION OF POLYGONUM PERSICARIA.

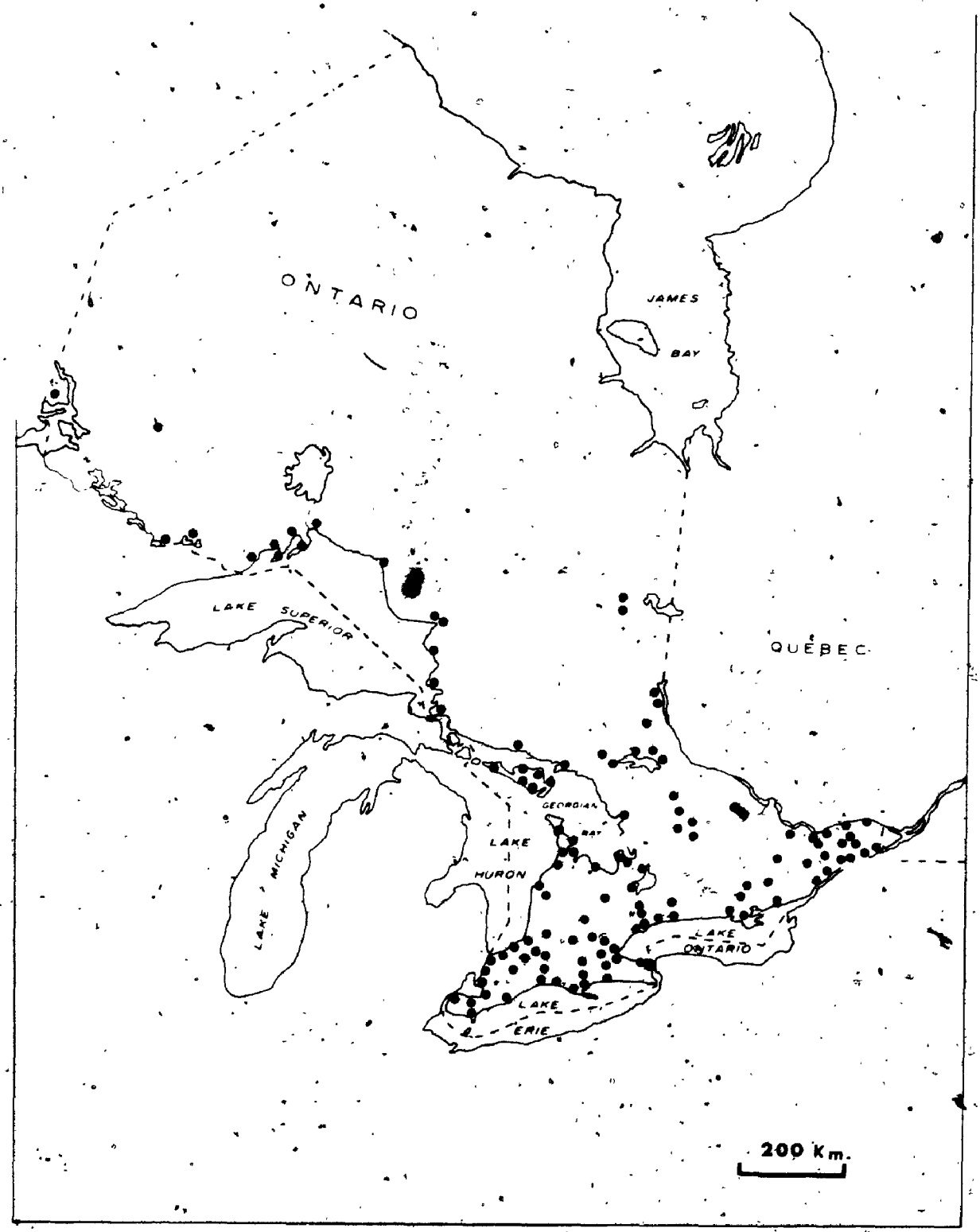

ONTARIO
JAMES
BAY
LAKE SUPERIOR
QUÉBEC
GEORGIAN
BAY
LAKE
HURON
LAKE MICHIGAN
LAKE
ONTARIO
LAKE
ERIE
200 km.

Table. II.1 List of herbaria visited for Survey II. International herbarium identifications codes are shown in brackets.

University of Guelph (OAC)

University of Western Ontario (UWO)

University of Toronto (TRT)

National Herbarium, Ottawa (CAN)

Department of Agriculture, Ottawa (DAO)

Laurentian University (SLV)

University of Windsor (no code at the time of writing)

Royal Botanical Gardens, Hamilton (HAM)

McMaster University (MCM)

University of Waterloo (no code at the time of writing)

Wilfred Laurier University (WLU)

Queens University, Kingston (QK)

Lakehead University (LKHD)

Université de Montréal (MT)

Jardin Botanique de Montréal (MTJB)

McGill University, Montréal (MTMG)

University of Michigan (MICH)

Michigan State University (MSC)

II.2.3 Survey IIIa. Distributions on three soil types and in three land use classes near Delaware, in the London area

Montgomery (1964), Frankton and Mulligan (1970) have shown that P. lapathifolium and P. pensylvanicum are known as serious weeds only from certain provinces, whereas P. persicaria tends to be an agricultural weed throughout its range. Information concerning precise distributions on different soils and land uses was lacking for the London area.

The major rural land uses in the London area were classified as agricultural land, riverbanks and bottomland, wasteland and woodland. It was decided to examine the distributions of the species on riverbanks in a separate study (Survey IIIb) for two reasons:

a) This habitat tends to be unidimensional, demanding a different sampling technique, thus preventing direct comparisons of the results with those from the other habitats.

b) The heterogeneity of river bottomland soils prevented classification with the soil types described below.

For the purpose of this survey it was necessary to establish working definitions of the major land use types:

1. Woodland. This category includes more or less natural woodland composed of mixed broadleaf/coniferous species with relatively undisturbed herb and shrub layers.
2. Agricultural land. Refers to land in use for the cultivation of one or more species other than trees.

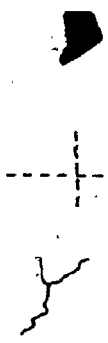
3. Wasteland. Includes land disturbed by man which is not forest or used for agricultural purposes.

The soils of south-western Ontario and Middlesex County have been classified broadly into sands, sandy loams, clay loams, clays, mixed soils of river bottomlands, silts, mucks and gravels (Anon. 1931). River bottomland soils are dealt with in Survey IIIb. Silts, mucks and gravels occupy a relatively small proportion of the soil types in the area and were omitted from the study. For the purpose of this study three soil types were recognized, each comprising of several subclasses (Anon. 1931). These were:

1. Sandy soils. Berrien sandy loam, Brookston clay loam with sand spot phase (more sand than clay in the study area), Fox fine sandy loam, Oshtemo sand, Plainfield sands.
2. Loamy soils. Guelph loam, London loam, Parkhill loam, Burford gravelly loam.
3. Clay soils. Haldimand clay loam, Huron clay loam, Perth clay loam.

The area (approx. 35 sq. km.) chosen for this study (Survey IIIa) was sited near the village of Delaware (42°55'N 81°25'W). This area is illustrated in Figure II.7. Figure II.8 was taken from a map published by the Dept. of National Defence (indexed as St. Thomas 40 1/4 west half); it shows the topography, communities and road system. This area includes sandy, loamy and clay soils in approximately

FIG. II.7 SITE OF EXPERIMENTAL AREA IN SOUTH WEST ONTARIO.



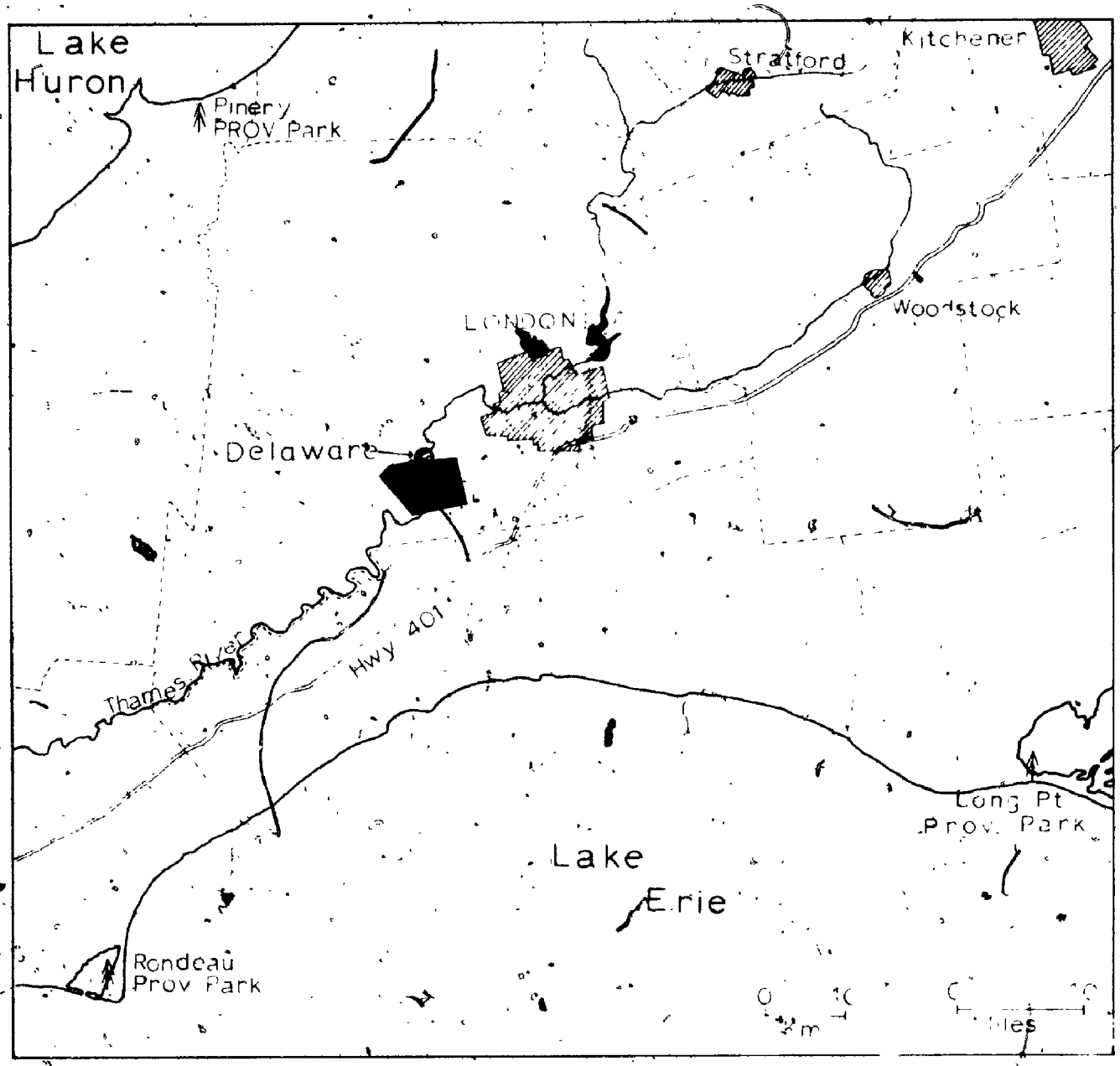
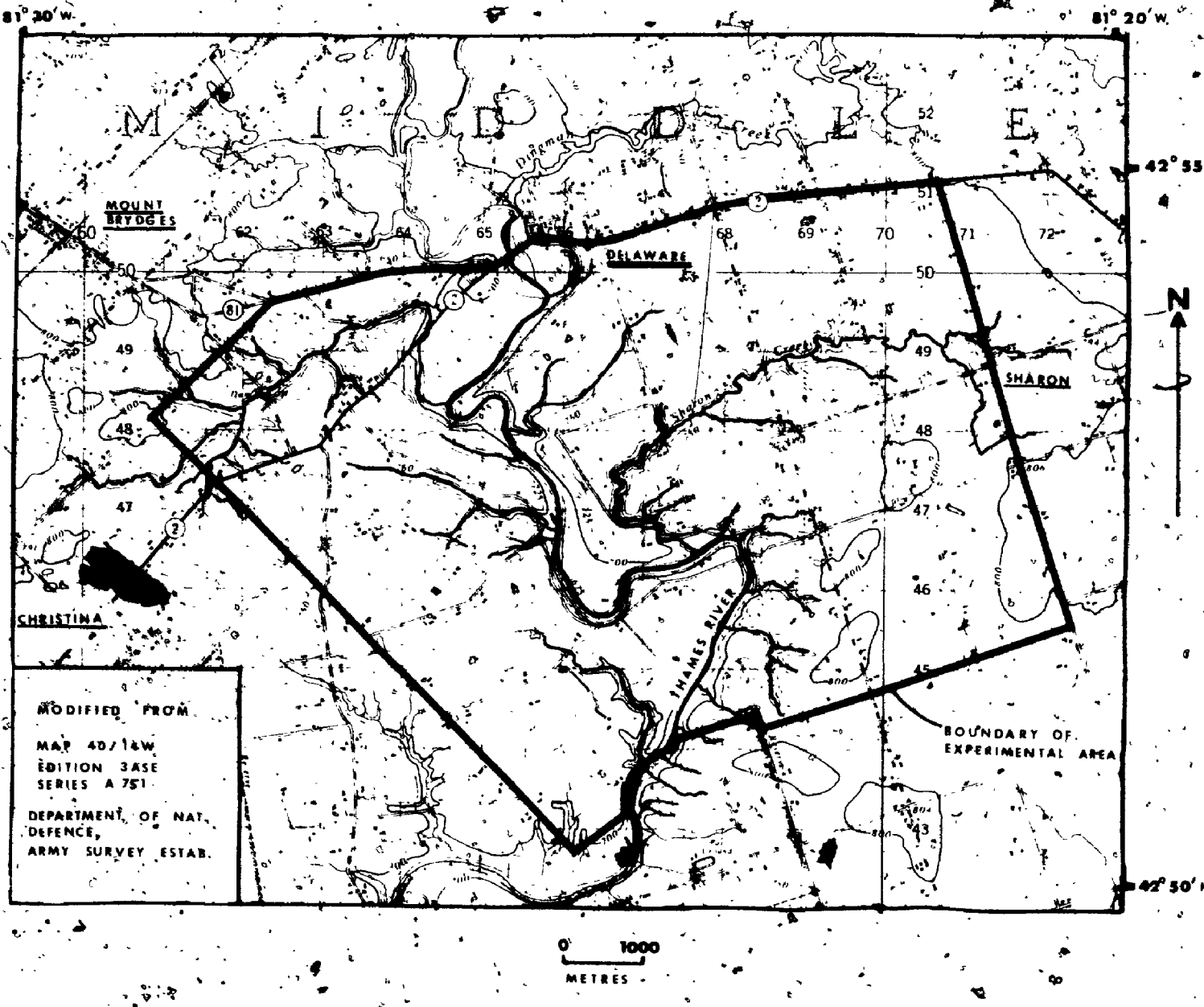

Lake
Huron
Pinery
PROV Park
Stratford
Kitchener
N
LONDON
Woodstock
Delaware
Thames River
Hwy 401
Long Pt
Prov. Park
Lake
Erie
Rondeau
Prov Park
0
10
km
0
10
Miles

FIG. IV.8 ROADS AND TOPOGRAPHY OF THE EXPERIMENTAL AREA.


81° 20' W.
81° 20' W.
42° 55' N.
42° 50' N.
MIDDLE
MOUNT BRYDGES
DELAWARE
SHARON
CHRISTINA
THAMES RIVER
BOUNDARY OF EXPERIMENTAL AREA
N
MODIFIED FROM
MAP 40/16W
EDITION 3ASE
SERIES A 751
DEPARTMENT OF NAT. DEFENCE,
ARMY SURVEY ESTAB.
0 1000
METRES

equally sized areas (Fig. II.9). The three land use types could be found without difficulty on each soil type (Fig. II.10).

One hundred sites (3 m. in diameter) were selected by restricted random sampling within each soil and land use type in the study area. Each site was located at least ten metres inside the boundary of the land use or soil type under study. It was examined to ensure that it fitted within the working definitions given earlier for soil type and land use classifications. The occurrence or absence of the study species was noted in each site during September 1969.

Data obtained from this survey were analysed by means of information analysis (Kullback, Kupperman and Ku 1962) and details are given in Appendices II.2 and 3.

II.2.4 Survey IIIb. Relative frequency along the Thames River

This survey was conducted in October 1969. The area of study consisted of the banks of the Thames River from Highway #2 at Delaware, southwestwards to the northern boundary of the Indian reserve near Muncey (see Fig. II.8). The procedure adopted was one of restricted random sampling along both banks of this stretch of the river, a total of approximately 13 km. Three randomly selected sites were used on each bank for each of the fifty 130 m. sections of the river. At each of these 300 sites, the presence or absence within a circular quadrat 1 m. in diameter of each of the three species of Rolygonum was recorded at a randomly

FIG. II.9 DISTRIBUTION OF MAJOR SOIL TYPES IN EXPERIMENTAL AREA.

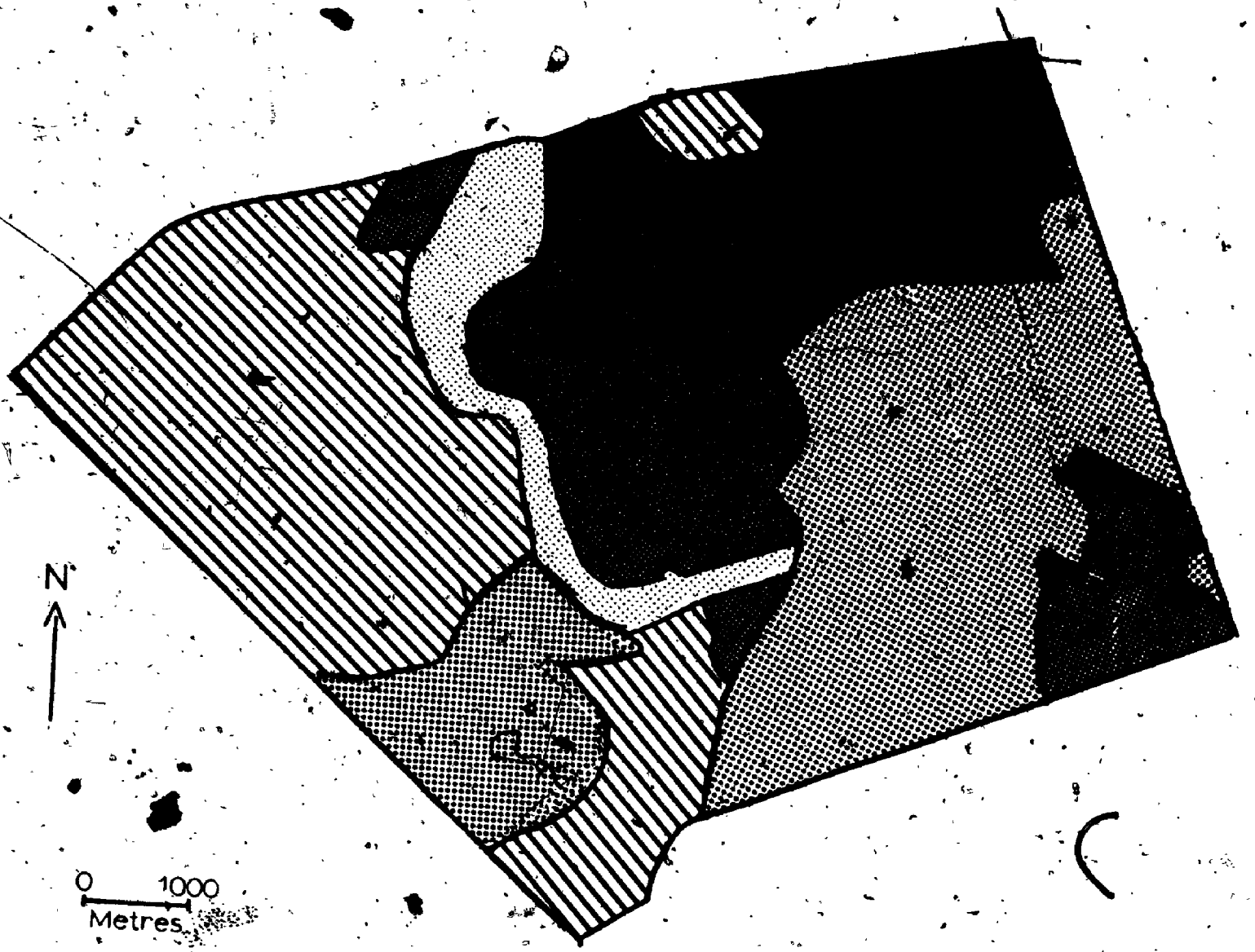
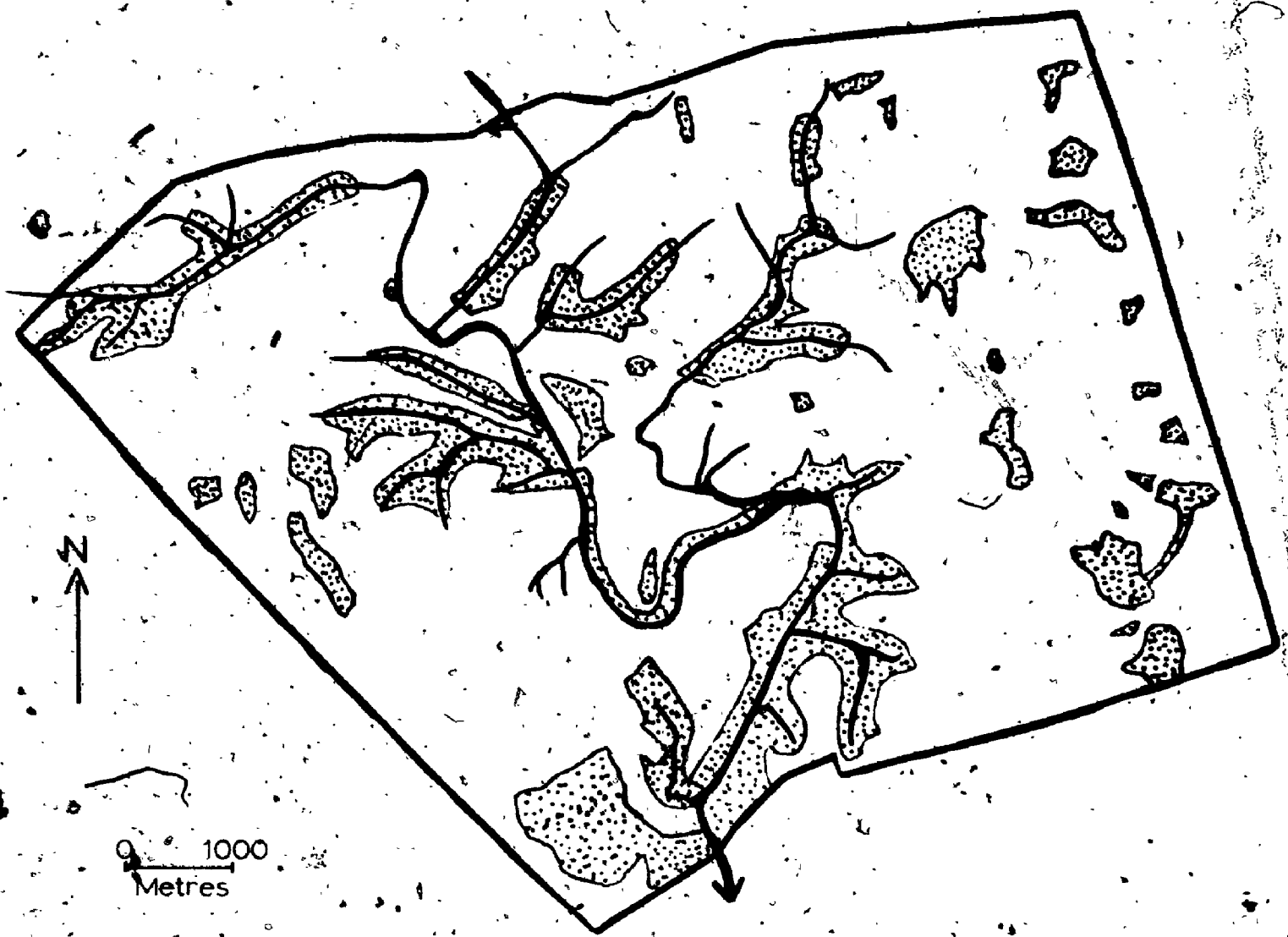

N
0 1000
Metres

FIG. II.10 DISTRIBUTION OF RIVERS, WOODLAND AND AGRICULTURAL LAND IN EXPERIMENTAL AREA.

woodland

agricultural land

river and tributaries


N
0
1000
Metres

chosen distance from the waters edge. The data were analysed by means of information statistic. Details are given in Appendix II.4.

II.2.5 Survey IV. Distribution within gravel banks

During Survey IIIb it was noted that the three species of Polygonum frequently occurred on river gravel banks. Survey IV was designed to find if the three species grow equally well in environmentally different habitats (should they exist) within the gravel banks. The technique used was as follows:

a) Attempt to identify smaller habitats (zones) within gravel banks, based on descriptions of location, soil and vegetation gathered from a large number of quadrats.

b) Find and compare the mean biomass (of each species of Polygonum) per unit area for each of the previously identified zones.

Results may show that; (i) all species exhibit the same trends (e.g. all species produce a large biomass in the same zones and small in the remaining ones), alternatively (ii) species differences may exist (e.g. large biomass for species A in zone 1, small in zone 2; small biomass for species B in zone 1, large in zone 2).

The survey was conducted in September, 1972 at a time when river levels were low.

II.2.5a Choice of sites

The banks of the Thames River in the London area were examined for possible study sites and eventually three

gravel banks were chosen. The selection criterion was that they should consist of large expanses of loose gravel, the habitat of interest to this study. The locations of the gravel banks are shown in Fig. I.2 (Chapter I), and are more precisely described below.

Gravel bank 1. On the east bank of the North Branch of the Thames River, 50 m. downstream from the Richmond St. bridge, London (Dept. of National Defence and Army Survey Estab. Map; S; Edition 3MCE, series A751, grid ref: 781622).

Gravel bank 2. On the east bank of the North Branch of the Thames River at the western end of Victoria St., Gibbons Memorial Park, London (Dept. of National Defence and Army Survey Estab. Map; Edition 3MCE, series A751, grid ref: 779606).

Gravel bank 3. On the east bank of an island in the Thames River, approximately midway between the Kilworth and Komoka Bridges, near London (Dept. of National Defence and Army Survey Estab. Map; Edition 3ASE, series A751, 40 1/4 W., grid ref: 670545).

Photographs were made of the three gravel banks during high and low water periods (Plates 1, 2 and 3). These plates show a dramatic and rapid change in water level.

II.2.5b Sampling techniques

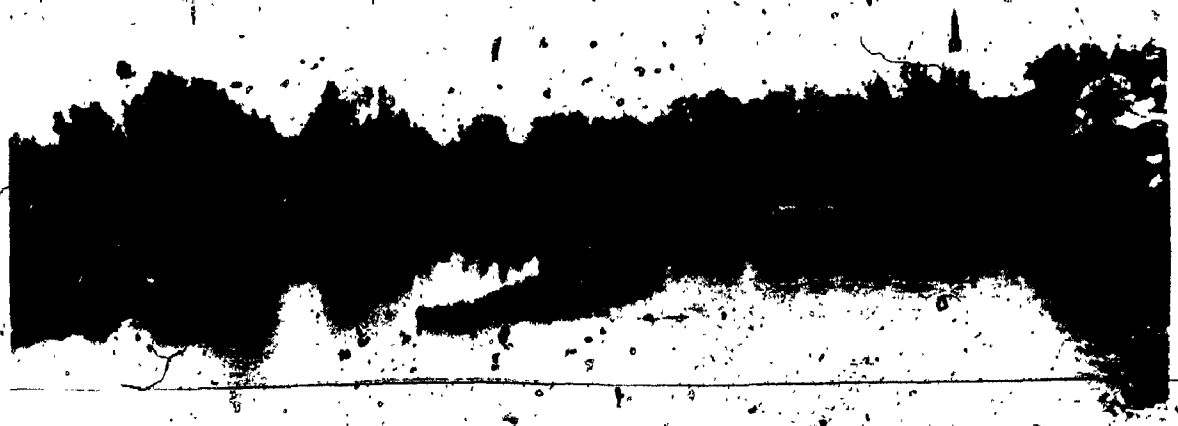
Rectangular study areas (each 20 x 10 m.) were marked out by means of pegs on gravel banks 1 and 2. The study areas extended longitudinally from the water's edge to the

PLATE 1

Photographs of gravel bank 1 (see Survey IV, Chapt. II) during high and low autumn water levels. Views from Richmond St. bridge, London looking downstream.

Upper: High water conditions (October 22nd, 1972)

Lower: Low water conditions (October 12th, 1972)



2 5

OF/DE

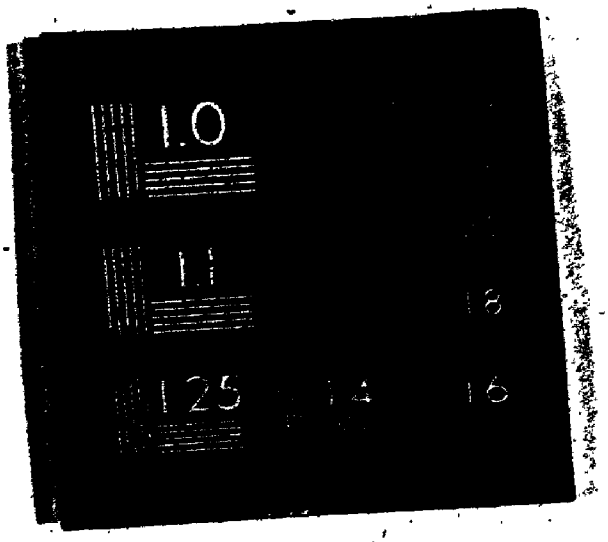


PLATE 2

Photographs of gravel bank 2 (see Survey IV, Chapt. II) during high and low autumn water levels. Views from Gibbon's Memorial Park, London looking upstream.

Upper: High water conditions (October 22nd, 1972)

Lower: Low water conditions (October 12th, 1972)

PLATE 3

Photographs of gravel bank 3 (see Survey IV, Chapt. II) during high and low water levels in autumn. Views from a point between the Kilworth and Komoka bridges, Middlesex Co. looking upstream.

Upper: High water conditions (October 22nd, 1972)

Lower: Low water conditions (October 12th, 1972)

back of the gravel bank, distances of approximately 20 m. Gravel bank 3 was relatively narrow and in this case the study area was a 5 x 40 m. rectangle, running 40 m. along the water's edge to a distance of 5 m. away from it. A grid of 200 squares (1 x 1 m.) was superimposed upon each of the three study areas and twenty grid squares selected by means of random number allocations from each. By this method 60 quadrats in total (each 1 x 1 m.) were sited randomly on the gravel banks. A sampling intensity of 0.1 (sixty 1 x 1 m. quadrats per 600 sq. m. of study area) was considered adequate for this study (Dr. L. Orlóci, pers. comm.). The quadrat size (1 x 1 m.) was sufficiently large for the inclusion of at least some plants from the generally sparsely vegetated gravel bank within each quadrat.

II.2.5c Data

Location, vegetation and soil variables were measured for each quadrat. Each quadrat location was described by two variables; the vertical height of the centre of the quadrat above the water level at the time of the survey (a) and the horizontal distance between the centre of the quadrat and the water's edge (b). The vertical height was calculated by means of a pocket transit*

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* Pocket transit by Wm. Ainsworth and Sons, Denver, Colorado.

and the horizontal distance estimated by geometric calculations knowing (a), (c) and that the angle ac is a right angle (see Fig. II.11). Only in 12 quadrats out of the 60 did (b) differ by more than 0.1 m. from (c), hence inaccuracies due to the assumption that (c) is an even slope were ignored.

Observations indicated that two vegetation criteria varied considerably on the gravel banks and these were subsequently used to describe quadrats. Firstly, the vegetation was dense in some parts of the gravel bank and very sparse in others. The total dry weight of vegetation (including underground organs) within each quadrat was used to describe this variable. Every plant within each quadrat was dug up, identified, dried (60°C for two weeks) and weighed. The second variable was the number of species within each quadrat. This variable was chosen to reflect the observation that in some areas dense vegetation was made up for one or few species/sq. m. only (notably Agrostis stolonifera or Phalaris arundinacea) and in others the dense vegetation was made up of 35 or more species/sq. m. A list of species found in the study areas on the three gravel banks is given in Appendix II.5. In addition to the two variables measured above, the dry weight of each species of Polygonum was recorded for each quadrat and used in the final analysis described later.

Several soil variables were measured for each quadrat. These included water content, gravel and clay

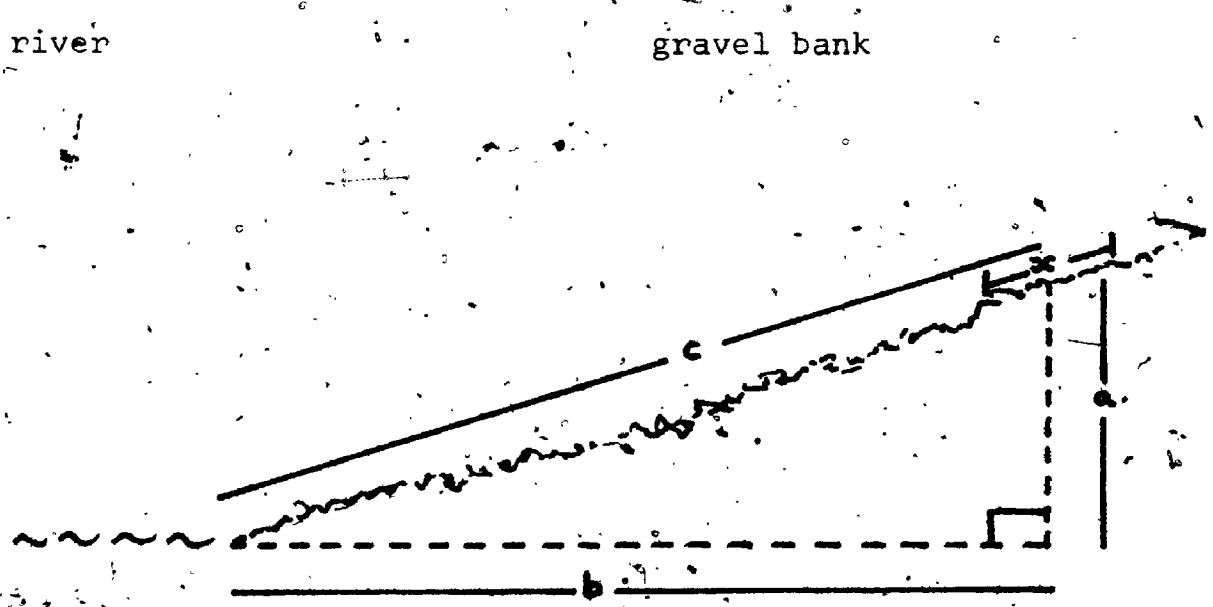


FIG. II.11 VARIABLES USED TO DESCRIBE THE LOCATION OF QUADRAT (x) IN RELATION TO THE RIVER.

Key: (x) the quadrat (1 x 1 m.), (a) vertical height above water level, (b) horizontal distance from the river, (c) distance from the river.

contents, pH level and nutrient status. A soil core (approximately 5 x 5 cm. and 20 cm. deep) was taken from the centre of each quadrat. The soil within each core was thoroughly mixed and a small sample taken for chemical tests, the remaining soil was placed in a polythene bag until the physical properties could be analysed. The chemical analyses were carried out immediately after collection using a Helige-Truog Soil Combination Kit. Qualitative measurements were made for the following nutrients: phosphorus, potassium, calcium, nitrate, ammonium, sulphate and chloride. The Helige-Truog scales recorded the quantities of these nutrients as "very low", "low", "medium", "high" or "very high". For the purposes of this study these ratings were reclassified by code values 1 to 5, respectively. The Helige-Truog Soil Combination Kit was also used to estimate the pH of the soil from each quadrat. The soil not used for chemical analysis was used in the physical analysis. It was weighed soon after collection, dried (60°C for two weeks) and reweighed. The loss in weight between the first and second weighings was recorded as the percentage water content of the fresh soil. The dry soil was sieved into three fractions described in this study as "gravel" (particles >2.00 mm. in diameter), "sand" (particles <2.00 mm., >0.11 mm. in diameter) and "clay" (particles <0.11 mm. in diameter). Organic material, silt and stones were included in these fractions. Each soil

fraction was weighed and the three sets of values were recorded as percentages of the fresh soil weights. The raw data are given in Appendix II.6.

II.2.5d Statistical methods

The data obtained in the survey were analyzed to determine the presence of possible discontinuities within the gravel bank habitat. The appearance of such discontinuities would justify the classification of quadrats into natural groups and support the "community concept" that vegetation and habitats exist as discrete, well defined types. Reduction of the mass of data to a few natural quadrat groups (zones) would then facilitate a comparison with the distribution of the three Polygonum species. The absence of discontinuities would lend support to the "continuum concept" which holds that vegetation varies continuously and is not naturally differentiated into natural groupings. A discussion of the two theories concerning the nature of vegetation is given by McIntosh (1967).

Several variables were omitted from the following analyses as they did not vary at all or very little. These were pH (7.5-8.0), phosphorus levels ("very low", one record; "low"), chloride levels ("very low"), sulphate levels ("very low", one record; "medium") and calcium levels ("very high"). The remaining eleven variables (dry weight records for each species of Polygonum were excluded) were used in the following analyses.

A principal component analysis was applied to the data in order to show interrelationships between quadrats and to allow visual interpretation of the sample for quadrat groups. In the analysis each quadrat was first placed in a multidimensional framework on the basis of the eleven parameters or attributes which described it. This scatter of points representing quadrats was then searched for the presence of axes (components) along which the points would show the greatest variance (Pielou 1969). After the first axis had been extracted a second was sought along which the points showed the next greatest variance. The second and subsequent axes were subject to the restriction that they were orthogonal to the earlier axes.

The principal component analysis was carried out by means of a computer program named PCAR (Orlóci 1975). The data were not standardized as is sometimes done when the parameters are measured in several different units. Standardization tends to give variables with low variances a greater influence than if unstandardized data were used. The justification of a standardization in this context is, therefore, debateable (Pielou 1969). The latent roots of the first three component axes accounted for 63.3% of the total variance. The first three axes were, therefore, considered adequate to describe relationships between the points. Ideally the first three axes should be plotted on a three dimensional framework. This is impractical in this thesis and they are shown as three two dimensional

graphs (Figs. II.12-14). The correlation coeffitients between the first three latent vectors and each of the eleven variables are given in Table II.2.

The absence of any obvious groups of quadrats seems to support the hypothesis that the gravel bank is a continuously varying habitat. Grouping of quadrats by a classification would be arbitrary. However, for the purpose of this study such arbitrariness was not considered inappropriate. The aim of the classification was merely to reduce the mass of data by uniting similar quadrats into a number of groups which could then be analyzed for Polygonum content. Statements concerning descrete zones within the gravel banks could not be made.

A sum of squares agglomerative classification (Orloci 1967) was used to form five quadrat groups. In this classification, unions are made between points (quadrats) or groups of points in a multidimensional framework. Unions are made only if the within-group dispersion in the union group is less than it would have been had either of the component groups united with any other group. Within group dispersion is measured by the sum of squared distance between every point and the group's centroid. The centroid, a pseudo point, is the "average" quadrat of the group, which has its co-ordinates as the mean of each variable (Pielou 1969). Unions are made until all quadrats are eventually placed in one group. A hierarchical dendrogram could then

FIG. II.12 FIRST AND SECOND PRINCIPAL COMPONENT AXES FOR A SWARM OF POINTS REPRESENTING QUADRATS LOCATED ON GRAVEL BANKS AND DESCRIBED BY 11 ENVIRONMENTAL VARIABLES.

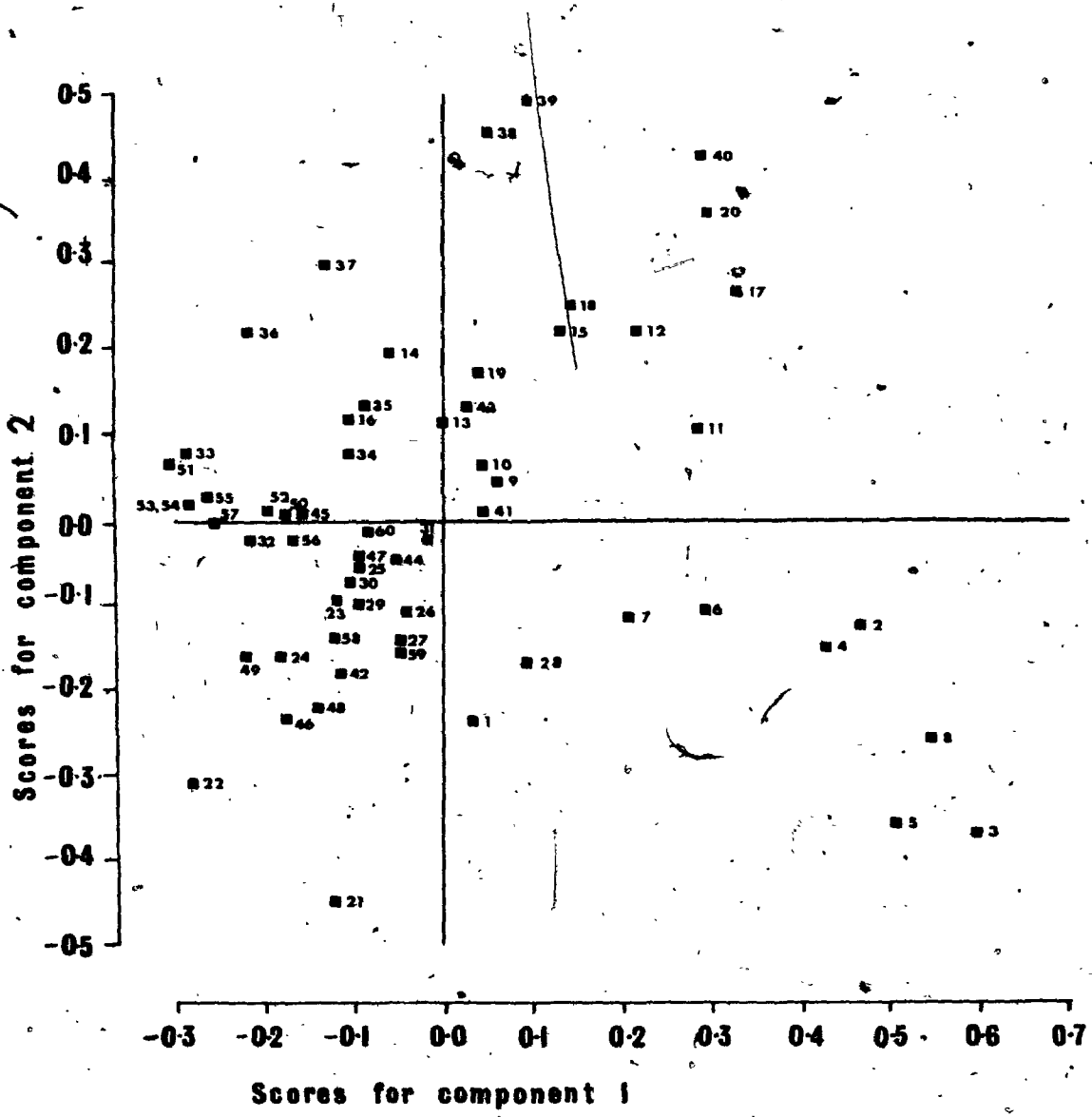
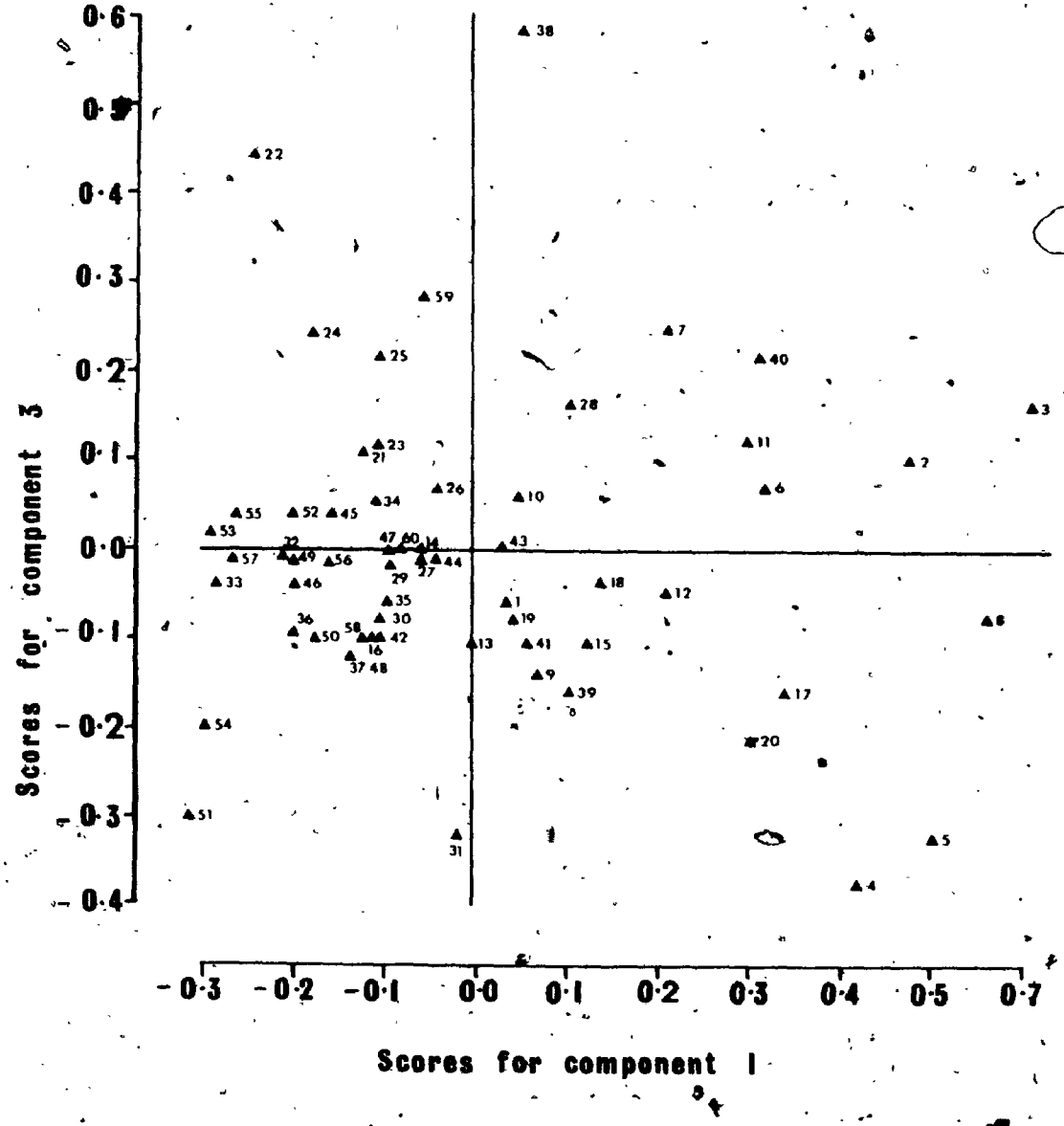

Scores for component 2
0·5
0·4
0·3
0·2
0·1
0·0
-0·1
-0·2
-0·3
-0·4
-0·5
-0·3
-0·2
-0·1
0·0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
Scores for component 1

FIG. II.13 FIRST AND THIRD PRINCIPAL COMPONENT AXES FOR A SWARM OF POINTS REPRESENTING QUADRATS LOCATED ON GRAVEL BANKS AND DESCRIBED BY 11 ENVIRONMENTAL VARIABLES.


0·6
0·5
0·4
0·3
0·2
0·1
0·0
-0·1
-0·2
-0·3
-0·4
Scores for component 3
-0·3 -0·2 -0·1 0·0 0·1 0·2 0·3 0·4 0·5 0·7
Scores for component 1

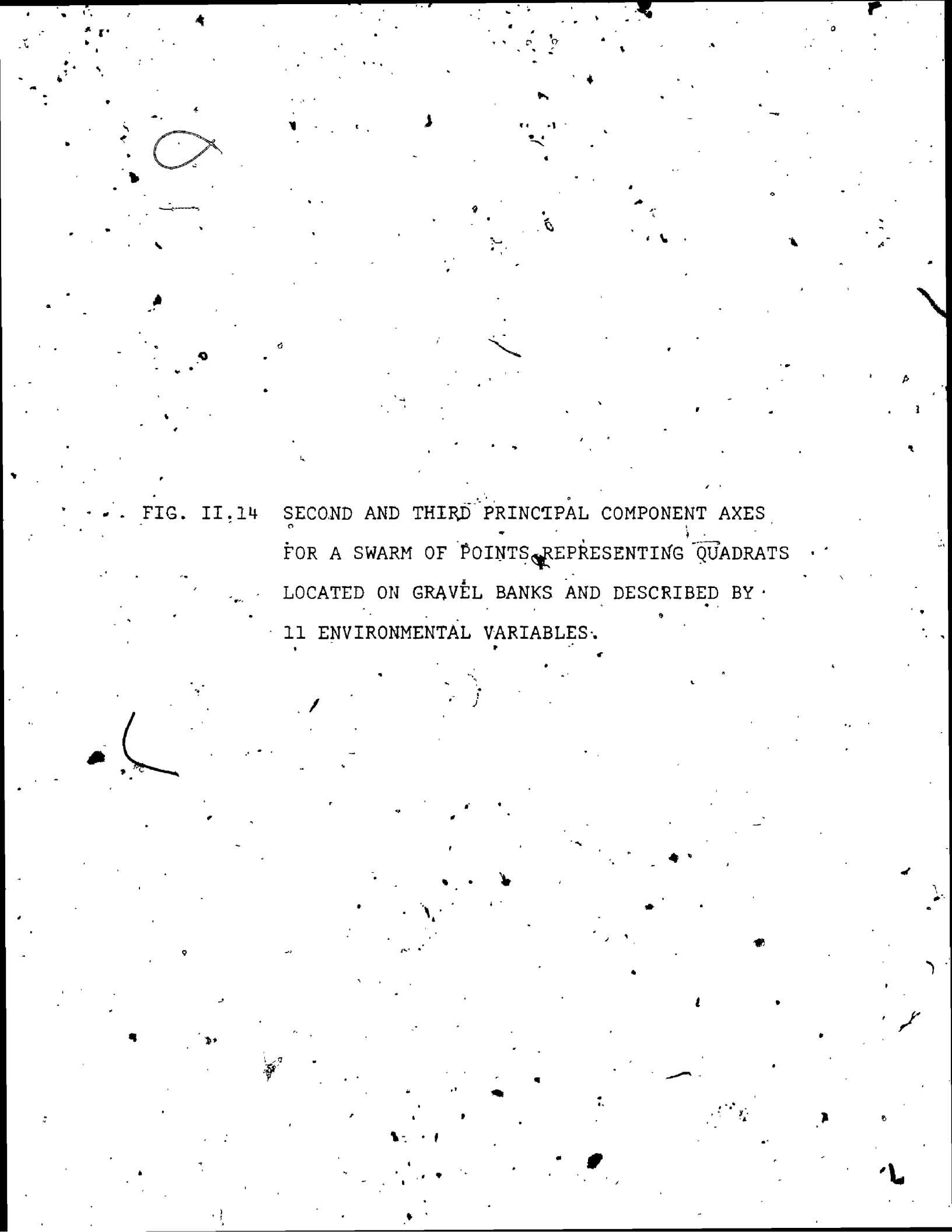


FIG. II.14 SECOND AND THIRD PRINCIPAL COMPONENT AXES FOR A SWARM OF POINTS REPRESENTING QUADRATS LOCATED ON GRAVEL BANKS AND DESCRIBED BY 11 ENVIRONMENTAL VARIABLES.

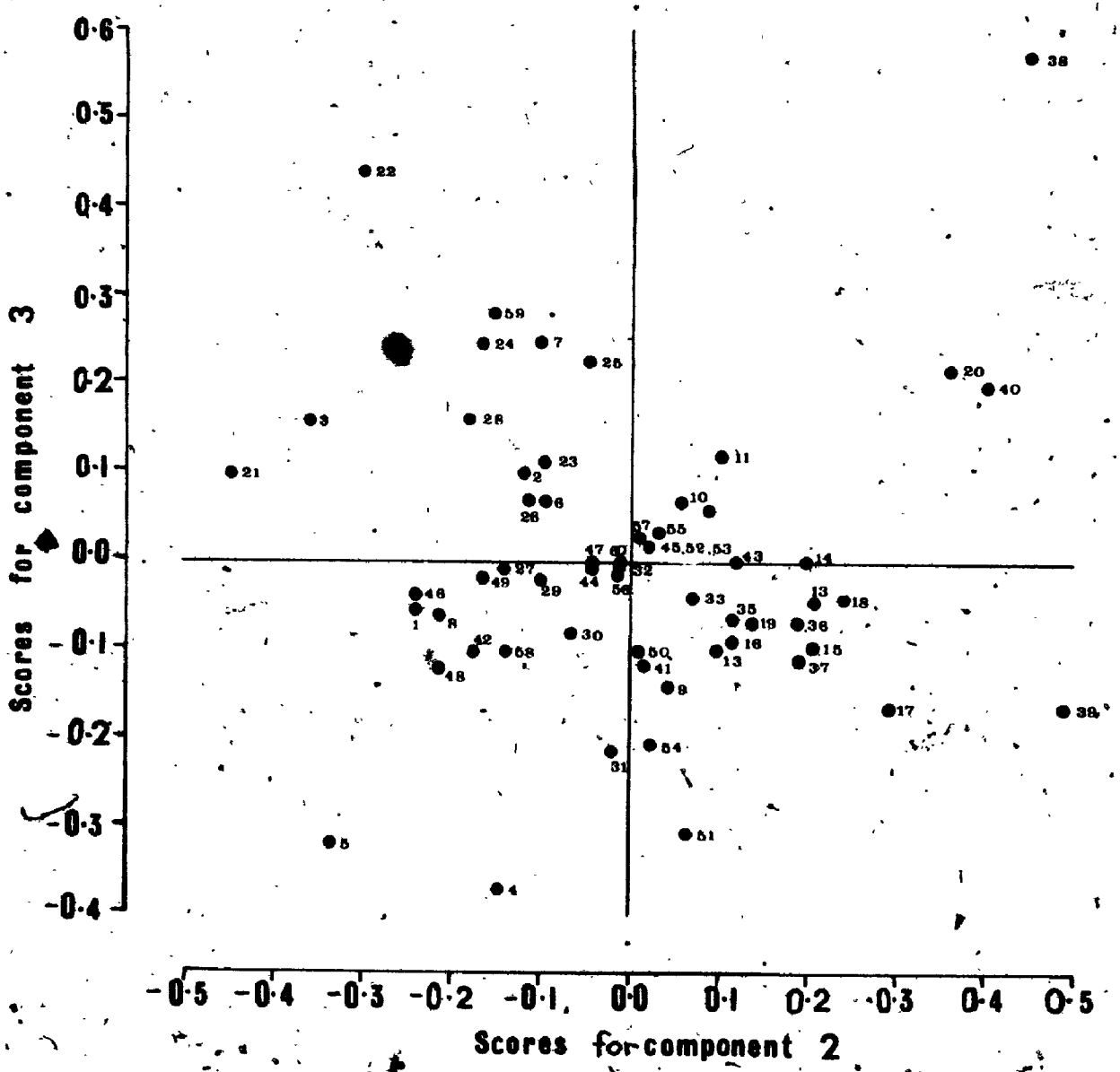

0·6
0·5
0·4
0·3
0·2
0·1
0·0
-0·1
-0·2
-0·3
-0·4
Scores for component 3
-0·5 -0·4 -0·3 -0·2 -0·1 0·0 0·1 0·2 0·3 0·4 0·5
Scores for component 2

Table II.2 Correlation coefficients of the eleven environmental factors with the three principal latent vectors. Values underlined show high correlations between factors and vectors.

	Latent Vector 1	Latent Vector 2	Latent Vector 3
Dry weight of vegetation/quadrat	0.17	-0.08	<u>0.52</u>
Number of species/quadrat	0.40	-0.06	-0.01
Vertical height above river	-0.26	0.28	0.04
Horizontal distance from river	0.11	<u>0.54</u>	-0.02
Chemical properties of soils:			
Potassium	-0.04	-0.15	<u>0.58</u>
Nitrate	-0.01	0.20	<u>0.47</u>
Ammonium	-0.01	-0.30	0.36
Water content of soil	0.37	-0.40	-0.14
Physical properties of soils:			
Gravel	<u>-0.50</u>	-0.25	-0.04
Sand	0.35	<u>0.46</u>	0.12
Clay	<u>0.46</u>	-0.21	-0.11

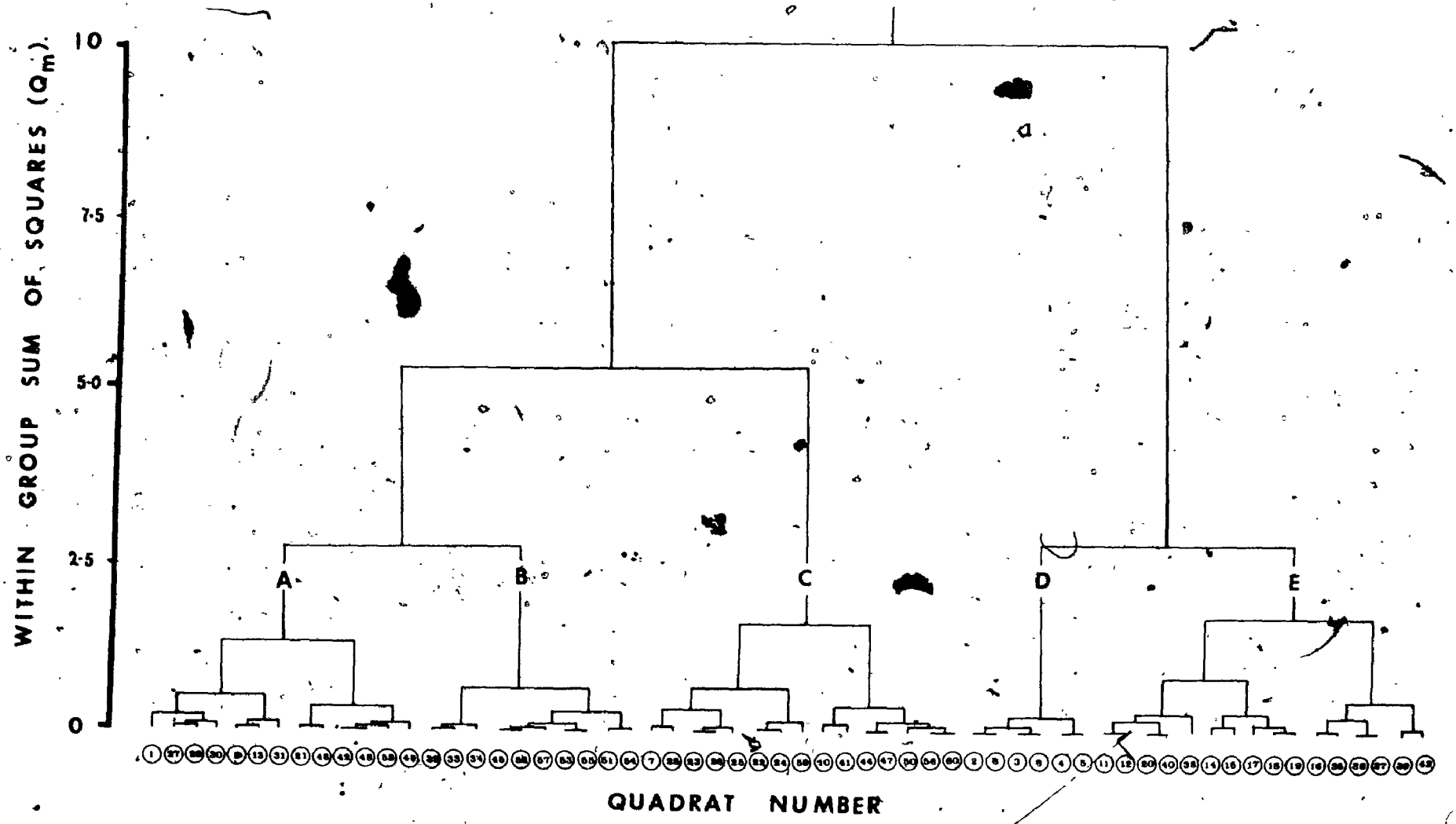
be drawn to show the levels of union between groups. Orlóci (1967) has shown that "standardized distances" are frequently a more desirable estimate of the distance between two points, than absolute distances. Standardized distances were used in the analysis of the gravel bank data.

A sum of squares agglomerative classification was made possible by means of a computer program named SSA (Orlóci 1975). The hierarchical arrangement of groups of quadrats by this analysis allowed the construction of a dendrogram (Fig. II.15) which illustrates the degree of heterogeneity in the groups of quadrats. Values along the vertical axis indicate the sum of squares, rescaled on a scale from 0 to 10. A union at 0 represents the point at which two identical groups were united and 10 represents the heterogeneity value at the point of union between the two least similar groups.

Five groups of quadrats were selected from the dendrogram and labelled A to E. These groups were of approximately equal sizes and were later identified with real (but not discrete) habitat zones on the gravel banks. Mean values and standard errors for each of the sixteen variables were calculated for each of the groups and are shown in Table II.3.

Mean values for biomass/quadrat of each Polygonum species were calculated for each group. Zero entries were not used in these calculations due to the ambiguity arising from their interpretation. It was not known whether a zero value for a Polygonum species in a particular quadrat indicated the absence of propagules (a dispersive

FIG. II.15 DENDROGRAM SHOWING CLASSIFICATION OF 60 QUADRATS LOCATED ON GRAVEL BANKS INTO 5 GROUPS.


WITHIN GROUP SUM OF SQUARES (Q_m).
10
7·5
5·0
2·5
0
A
B
C
D
E
QUADRAT NUMBER

ble II.3 Means (and standard errors of means in some cases) of each variable for each quadrat group on the gravel bank.

adrat oup	Environmental Variables			
	Number of quadrats	Dry wt. of *P. lap.*/m^2 (g.)	Dry wt. of *P. pens.*/m^2 (g.)	Dry wt. of *P. pers.*/m^2 (g.)
A	13	25.8^{a}	26.2^{cd}	0.0
B	12	12.4^{a}	33.2^{cd}	4.1
C	14	17.5^{a}	45.6^{d}	3.0
D	8	64.5^{b}	2.9^{c}	3.7
E	13	21.3^{a}	38.5^{cd}	3.4

	% Frequency of *P. lap.*	% Frequency of *P. pens.*	% Frequency of *P. pers.*	Distance from water's edge (m.)
A	61.5	53.8	0.0	4.6 ± 4.9 { 1.0 ± 1.5, 10.3 ± 1.6
B	66.7	25.0	8.0	8.5 ± 5.5 { 4.1 ± 0.5, 14.7 ± 0.9
C	57.1	35.7	21.4	3.1 ± 2.4
D	75.0	75.0	12.5	5.1 ± 2.0
E	76.9	92.3	23.1	15.7 ± 2.8

Table II.3 (Continued)

Quadrat group	Environmental variables			
	Soil chemical properties			
	P	K	Ca	NO_3
A	v. low	v. low-low	v. high	v. low
B	v. low	v. low-low	v. high	v. low-low
C	v. low	v. low-med.	v. high	v. low-low
D	v. low	v. low-med.	v. high	v. low-low
E	v. low	v. low-low	v. high	v. low-med.

	NH_4	SO_3	Cl
A	v. low-med.	v. low	v. low
B	low	v. low	v. low
C	low-med.	v. low	v. low
D	low-med.	v. low	v. low
E	low	v. low	v. low

Table II.3 (Continued)

Quadrat group	Environmental variables		
	Height above water level (m.)	% water in soil	% gravel in soil
A	0.3 ± 0.2	9.1 ± 3.5	60.2 ± 11.5
B	0.9 ± 0.3	4.3 ± 3.3	67.0 ± 10.7
C	0.9 ± 0.3	5.3 ± 2.2	56.9 ± 15.3
D	0.2 ± 0.1	19.4 ± 6.9	19.8 ± 15.1
E	0.6 ± 0.3	4.2 ± 2.0	26.6 ± 18.9

	% Sand in soil	% Clay in soil	pH of soil
A	28.4 ± 10.8	1.0 ± 0.6	7.5 - 8.0
B	28.6 ± 9.5	0.8 ± 0.4	7.5 - 8.0
C	36.3 ± 14.3	1.2 ± 0.4	7.5 - 8.0
D	47.5 ± 10.1	13.3 ± 7.5	7.5 - 8.0
E	66.9 ± 19.0	2.5 ± 2.4	7.5 - 8.0

Table II.3 (Continued)

Quadrat group	Environmental variables	
	Dry wt. of vegetation/m^2 (g.)	Number of species/m^2
A	284.3 ± 163.4	18 ± 8
B	158.8 ± 84.1	11 ± 6
C	637.2 ± 248.0	23 ± 7
D	597.6 ± 288.5	31 ± 6
E	358.0 ± 122.8	26 ± 13

Note 1. Dry weight values for species of Polygonum associated with the same letter were not significantly different ($P > 0.05$). Between species comparisons were not made.

Note 2. During analysis the qualitative terms for soil chemical properties (i.e. "very low" to "very high") were given numerical values. The mean ± 1 standard error have been retranslated into qualitative terms in this table.

feature) or no growth (an unfavourable habitat).

The biomass values for each of the quadrat groups were compared for each species separately. Plants of P. persicaria were relatively rare on the gravel bars, hence analysis of their mean biomass values was omitted due to small sizes. Bartlett's tests were applied to data for P. lapathifolium and P. pensylvanicum to test the homogeneity of the variances. The calculated χ^2 value for P. lapathifolium was marginally less than the $\chi^2_{\alpha;\nu}$ probability point at $\alpha = 0.05$ (see Appendix II.7). Further analysis was carried out using analysis of variance followed by individual comparisons of means using the Student-Newman-Keuls (S.N.K.) test (Sokal and Rohlf 1969). Bartlett's test showed considerable heterogeneity amongst variances for data of P. pensylvanicum. Analyses of variance were not used for these data; however, further analysis was made possible by means of an approximate F-test followed by individual comparisons of means using approximate t-tests described by Sokal and Rohlf (1969). Details of the results of these analyses are presented in Appendix II.7.

II.3 Results and discussion

II.3.1 World distributions

The shortcomings of constructing distribution maps by the method described above must be stated:

a) The lack of manuals from certain areas or their unavailability to the author.

b) The omission of certain species from the manuals.

c) The risk of misidentification.

d) The lack of detail of species ranges within the area embraced by a manual.

Despite the shortcomings, sufficient differences in distribution between the species are demonstrated to make the maps (Figs. II.1-3) useful.

At the present time, Polygonum lapathifolium and P. persicaria occur in most temperate regions throughout the world. The range of P. persicaria does not extend as far north as that of P. lapathifolium. P. pensylvanicum is largely restricted to eastern North America. It has been reported from a few localities outside of this range in Panama (Woodson and Schery 1960), Mexico, California (Abrams 1923), Cuba, Hispaniola (Urban 1964) and Alaska (Anderson 1959).

P. lapathifolium is believed to be indigenous to both Eurasia and North America, P. pensylvanicum to North America only and P. persicaria to Eurasia only (Fernald 1950). The earliest records of achene remains are for P. persicaria in Britain (Godwin 1952). Achene fragments have been discovered, dating from the last three interglacial periods and usually associated with human activity. Fragments of an achene of P. lapathifolium date back to the last full glacial period and many more achenes of this species have been found associated with human activities in Britain, dating from the Bronze Age to the present time.

The presence of both P. lapathifolium and P. persicaria in New Zealand, Australia, South Africa and South America is due to introductions made during historical times. Man has probably been instrumental in the dispersal of P. lapathifolium and P. persicaria from early times by creating habitats suitable for their growth and by dispersing their fruits in samples of crop seeds (Simmonds 1945) and possibly by using them as food species.

II.3.2 Distribution in Ontario

It is understood that distribution maps drawn from herbarium data have two main weaknesses:

a) Subjectivity in the collection procedure has often resulted in disproportionately large collections of rare, conspicuous or conveniently sized specimens or species and conversely few collections of common, inconspicuous species or those which do not lend themselves easily to collection or preservation.

b) Collections have not been made randomly throughout the province. There is a comparitive lack of specimens from relatively inaccessible places.

Similarities in morphology and conspicuousness between species of Polygonum would suggest that differences in the numbers of specimens collected between species genuinely reflect the natural abundance of the species. The lack of information resulting from few or no specimens collected from remote regions was partly compensated for by referring to local manuals, descriptions of occasional

collecting excursions into these areas and to manuals of adjacent regions. The numbers of specimens examined were;

Polygonum lapathifolium	429
P. pensylvanicum	141
P. persicaria	350

The sites from which these specimens were collected are shown in Figs. II.4-6. Many specimens from different herbaria were duplicates hence, the number of collection sites is lower than the values given above.

Polygonum lapathifolium is widely distributed in Ontario (Fig. II.4). Many specimens have been collected from the Great Lakes Basin both in Canada and the United States. The most northerly record (specimen CAN 244332) was collected from Big Trout Lake (53°49'N 89°53'W). Specimens collected in southern Ontario were usually from riverbanks, damp or disturbed agricultural land or wasteland. In the northern half of Ontario the species is usually described as occurring on sandy beaches of lakes or rivers or on exposed mud. It has been collected from all of the major bedrock types, soil types (except tundra soils), natural vegetation types (except tundra), land use types and climatic regions. The absence of specimens from the tundra around the shores of Hudson Bay may be due to the rarity of collectors from that region, especially as its presence has been recorded from tundra regions further north in Manitoba (Scoggan 1957). The species is also

common in the adjacent provinces of Manitoba (Scoggan 1957) where it has been collected as far north as 58°46'N 94°10'W, Quebec (Marie-Victorin 1964) to 52°12'N 78°12'W (CAN 246593) and the states of Minnesota (MacMillan 1892) and North Dakota (Stevens 1950).

Polygonum pensylvanicum has the most restricted distribution of the three species reaching the northern limit of its range in the southern half of the province (Fig. II.5). The most northerly collection point for a herbarium specimen viewed by the author (Herbarium of, University of Waterloo specimen number 718a) was Sudbury (46°30'N 81°00'W). The distribution in Ontario is patchy with three main centres of concentration (see Fig. II.5):

a) South of a line drawn from Toronto to Goderich.

b) East of a line drawn from Kingston to Renfrew.

c) The shoreline around Georgian Bay.

There are scattered colonies present at Nestorville 46°18'N 83°36'W (MICH 5165), Sudbury, 46°30'N 81°00'W (University of Waterloo, specimen 718a) and North Bay 46°19'N 79°28'W (TRT 16735). Baldwin (1958) has reported that it is absent from the agricultural regions associated with the Great Clay Belt of northern Ontario.

Visual comparisons of distribution were made with soil and land use distributions (Webber and Hoffman 1968) and climatic data from Brown, McKay and Chapman, 1968. (Transparent overlays of these two factors are provided inside the back

cover of this thesis). The distribution of P. pensylvanicum closely matches the distribution of clay, loam and sandy soils which form the principal farming areas in Ontario. Exceptions are that this species appears to be absent from farming areas of the Clay Belt and the Grey County Highlands. It is absent from Precambrian, organic and tundra soils.

The distribution closely matches a number of mean annual isograms for several climatic parameters which have similar distributions to each other.

a) Mean daily temperature, >4°C (42°F)

b) Duration of the growing season, >185 days

c) The number of Growing-degree days, >3000

d) The number of consecutive frost free days, 120

e) The dates of the last and first frosts (not later than May 31st nor earlier than September 25th respectively).

P. pensylvanicum has been recorded for most of the adjacent provinces and states. Scoggan (1957) reports only one specimen from Manitoba (50°41'N 100°00'W). It has been recorded from North Dakota (Stevens 1950), Minnesota (MacMillan 1892), Ohio (Weishaupt 1971), New York State (Wiegand and Eames 1926; House and Alexander 1927) and Quebec (Marie-Victorin 1964).

The distribution of P. persicaria (Fig. II.6) is mostly restricted to the southern half of the province but this species occurs further to the north than P. pensylvanicum (Fig. II.5). The most northerly specimen examined was

collected from Sioux Lookout, 50°06'N 91°55'W (CAN 286586).

Baldwin (1958) reports that P. persicaria is rare on the Great Clay Belt; however, herbarium specimens indicate its presence on each of the clay plains of Kenora, Dryden, Thunder Bay, Kapuskasing and New Liskeard (Fig. II.6). These regions are also the principal farming areas in northern Ontario and most habitats given on the specimen sheets refer to cultivated land. In southern Ontario, the species has been recorded from all soil types including those of Precambrian deposits.

Several isograms match the northern limit of distribution for this species.

a) Mean daily temperature, >1°C. (34°F)

b) Duration of the growing season, >165 days

c) The number of growing degree days, >2300

d) The number of consecutive frost free days, >100

e) The dates of the last and first frosts (not later than June 5th nor earlier than September 10th)

Information concerning the climate of northern Ontario was derived from Chapman and Thomas (1968).

P. persicaria has been reported from most adjacent provinces and states; Manitoba as far north as 50°59'N 96°59'W (Scoggan 1957), North Dakota (Stevens 1950), Indiana (Deam 1940), Ohio (Weishaupt 1971), New York State (House and Alexander 1927; Wiegand and Eames 1926) and Quebec (Marie-Victorin 1964).

II.3.3 Survey IIIa

Table II.4 shows the nine land use/soil type combinations that were examined. The number of occurrences of each of the three species in one hundred quadrats is given for each combination.

P. lapathifolium is a rare species compared with P. persicaria. Occurrences were only recorded from agricultural land on sandy soils (cornfields) and wasteland on sandy and loam soils (ditches, a farmyard, a pathway and a field edge). It was consistently absent from clay soils and from woodlands.

P. pensylvanicum did not occur at any sites regardless of soil type or land use.

P. persicaria was a frequent species in agricultural land and wasteland on all soil types.

An information test was applied to these data in order to determine whether the occurrence of P. persicaria on the three soil types was independant of two land use types (agricultural and wasteland). The results of this test (Appendix II.2) revealed a significant relationship between these two sets of factors. P. persicaria was more abundant on agricultural lands where these were situated on clay soils; however, in wasteland its frequency was higher on sandy soils. The application of information tests to 2 x 2 contingency tables showed significant ($P < 0.05$) heterogeneity between the soil types, regarding the frequency

Table II.4 Frequencies of *Polygonum* species on three soil types and three land uses near London, Ontario. The numbers refer to occurrences in 100 circular sites, 3 m in diameter.

	Soil Type		
	Sandy	Loam	Clay
P. lapathifolium			
agricultural land	1	0	0
waste land	4	2	0
woodland	0	0	0
P. pensylvanicum			
agricultural land	0	0	0
waste land	0	0	0
woodland	0	0	0
P. persicaria			
agricultural land	9	24	28
waste land	25	24	24
woodland	1	0	0

of P. persicaria. Occurrences on sandy soils did not differ from those on loam soils, neither did the frequency of occurrences on clay soils differ from those on loam soils; however, occurrences on clay and sandy soils differed from each other at the 5% level. The application of a test of linear proportions (Snedecor and Cochran 1967) indicated that there is a linear increase in the proportion of occurrences in agricultural lands progressing from sandy soils to clay soils (Appendix II.3). This result may reflect a direct response, partly determined by the types of crop grown on different soils.

The occurrence of P. persicaria was examined in various crop types. Out of a total of 300 samples, this species was noted from 7 cornfields (out of 146), 54 small grain crops such as wheat, barley, oats and rye (out of 85) and from 2 "other crops" (out of a total of 69). "Other crops" includes white beans, tomato, melon and tobacco fields. An information test indicated a significant relationship ($P = 0.05$) between the occurrence of P. persicaria and the type of crop species. A simultaneous test procedure (STP) using the information statistic was applied to locate the heterogeneity between crop species. This test took into account the total number of sites in each crop type and so the scarcity of a crop type would not affect the results of this test or provide misleading information. Small grained cereals gave significantly higher frequencies for the occurrence of P. persicaria than the other crop

types which were not significantly different from each other ($P > 0.05$); see Appendix II.3. Small grained cereals are usually grown on clay or loam soils in the study area. Corn and tobacco crops are usually heavily sprayed with herbicides (such as Atrazine) to which most species of Polygonum are sensitive.

II.3.4 Survey IIIb

The occurrence (in 300 sites) of P. lapathifolium, P. pensylvanicum and P. persicaria along a portion of the Thames are given below;

P. lapathifolium	49
P. pensylvanicum	22
P. persicaria	10

Contrary to its relative frequency on agricultural and wasteland, P. persicaria was the rarest of the three species along the riverbank habitat. P. lapathifolium was the most frequent and P. pensylvanicum of intermediate frequency. Information tests (Appendix II.4) indicated that these differences were significant ($P < 0.05$).

II.3.5 Survey IV

An ordination by means of a principal components analysis of 60 quadrats located on gravel banks and described by 11 variables did not show the existence of discrete clusters of quadrats. The latent vectors of the first three principal axes were strongly associated with the clay (+) and gravel (-) contents of the soil (1st axis);

the sand content (+) of the soil and the horizontal distance from the river (-) (2nd axis); and the dry weight of vegetation/m^2 (+) and the potassium level in the soil (+) (3rd axis).

These findings support the theory that vegetation exists as a continuum of change (see McIntosh 1967). An alternative reason for the apparent lack of discrete vegetation units may lie in the sampling technique. Grieg-Smith (1964) has shown that the detection of pattern in vegetation is very much determined by the size of quadrats. In this survey it is possible that the large quadrat size (1 x 1 m) needed to obtain good quantitative data for plants of Polygonum, was too large to detect small discontinuities in habitat factors.

Five quadrat groups (labelled A to E) were selected by means of a sum of squares agglomerative classification. The mean values for each variable were used to describe the characteristics and location of each quadrat group. This made possible the construction of a diagram for a model gravel bank (Fig. II.16). Values for the "horizontal distance from the river" fell within two clusters for groups A and B. This suggested that A and B each had two locations on the gravel banks as is shown in the second model (Fig, II.17). According to these models the structure of the gravel bank is as follows:

A ridge runs adjacent to the river's edge. The top of the ridge (group C) is well vegetated but the soil is

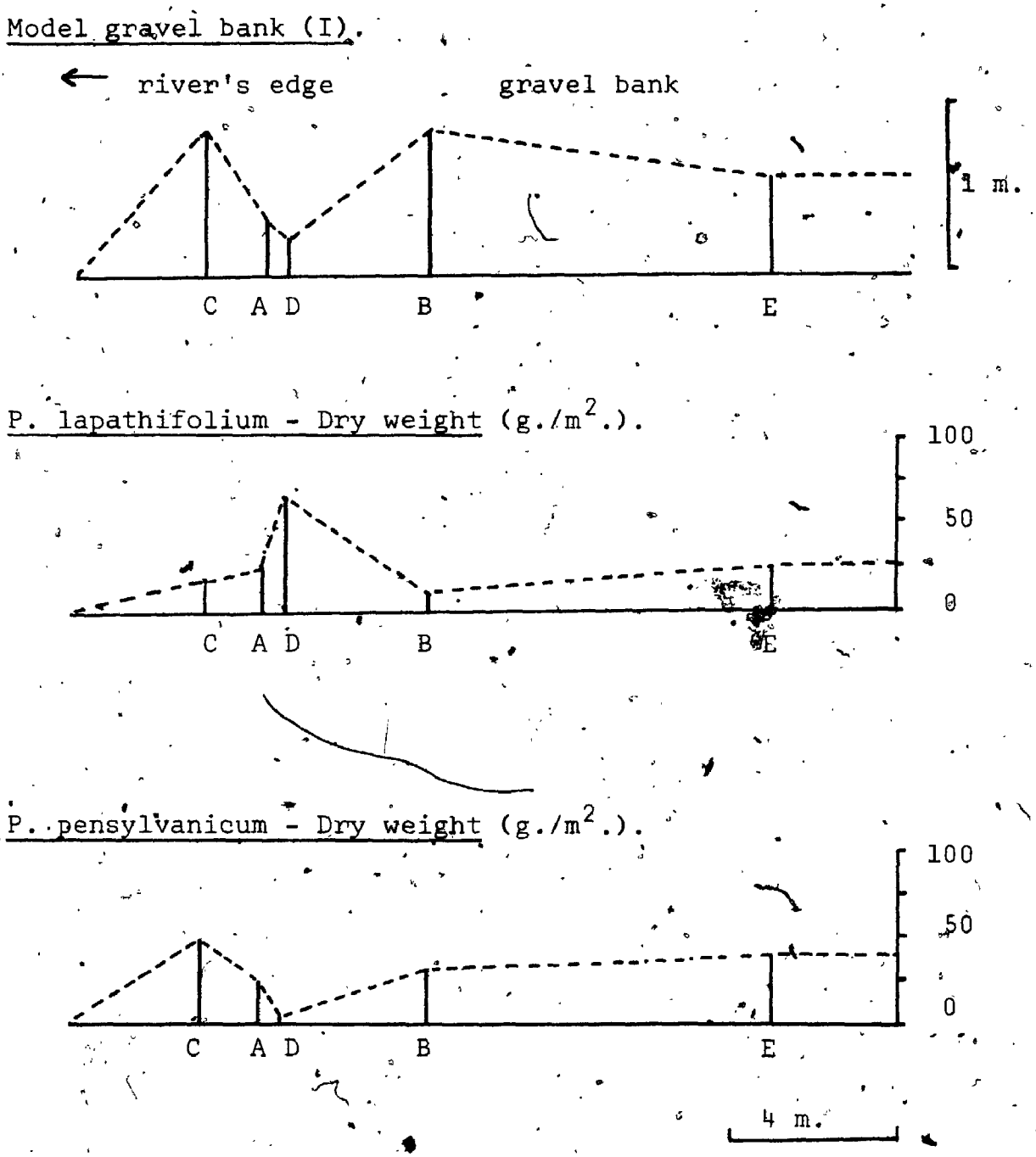
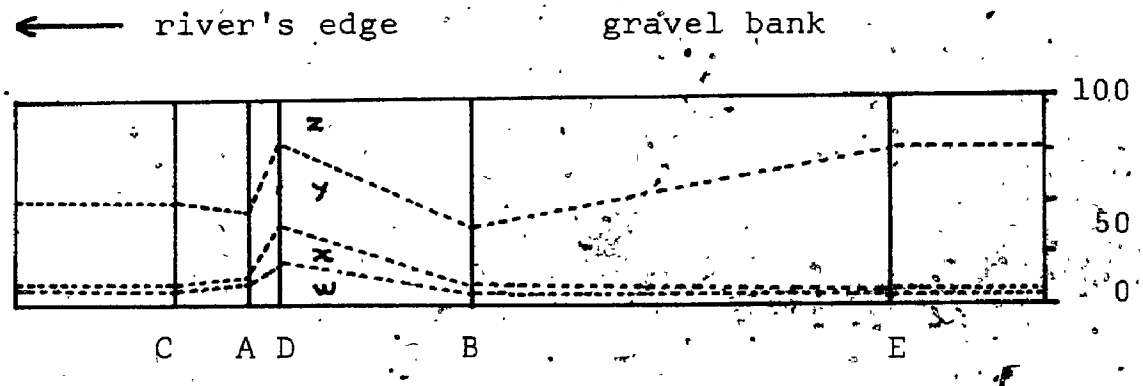


Fig. II.16. A model gravel bank constructed from mean values of location variables for each quadrat group, their relationships with mean values of other variables are also shown. (Continued on next page.)

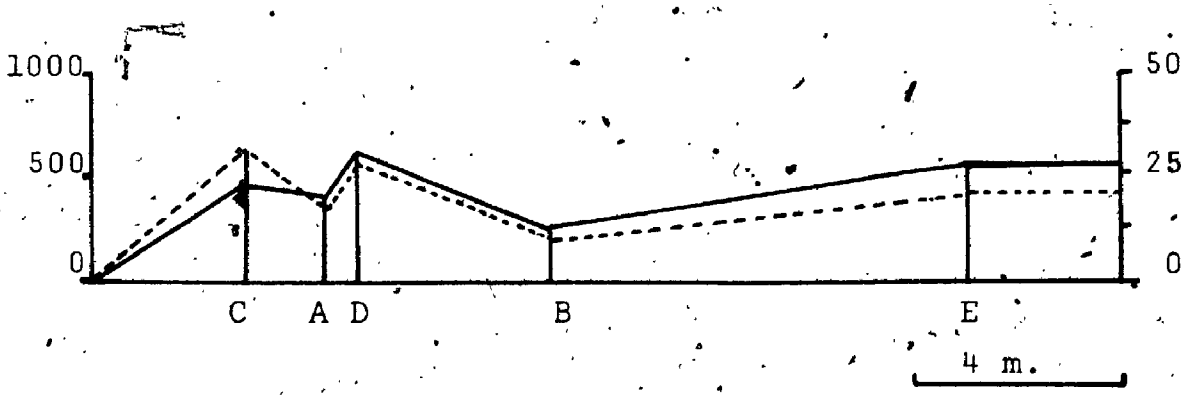
Fig. II.16 (continued)

Soil contents by weight (%).



Quantities for each variable should be read independently, they are not cumulative:
(w) water, (x) clay, (y) sand, (z) gravel.

Vegetation variables; dry weight, g./m^2. (broken line, scale on left), number of spp./m^2. (solid line, scale on right).



Letters refer to quadrat groups described in Table II.3.

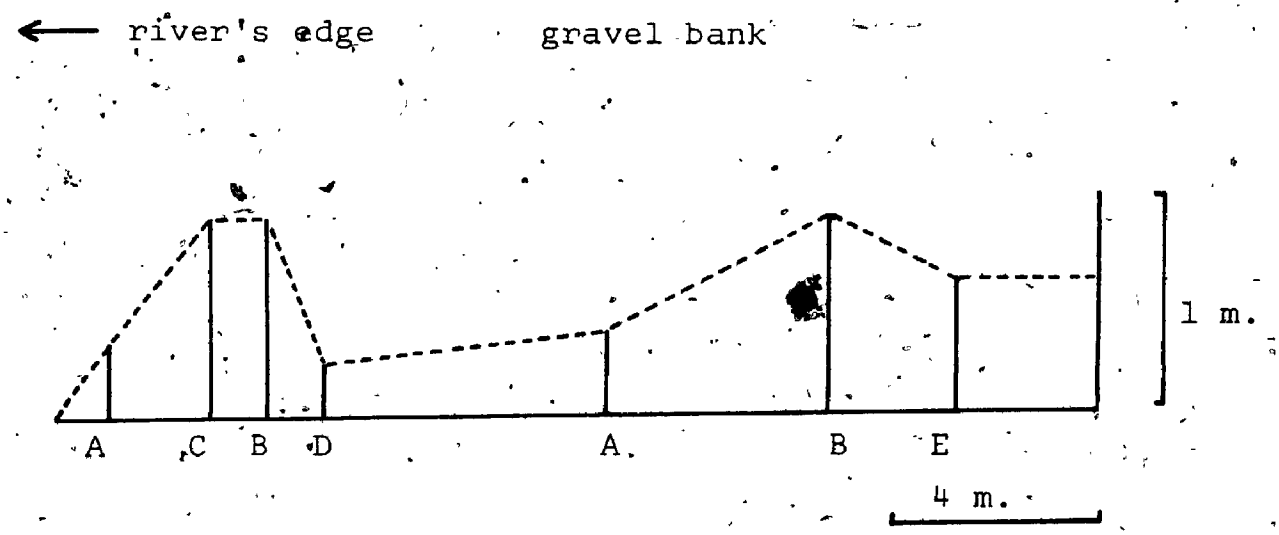


Fig. II.17. Model 2 — An alternative interpretation of data for construction of a model gravel bank. (See Survey IV, Results). Letters refer to quadrat groups described in Table II.3.

dry and composed of sand and gravel particles. On the river side of the ridge a low wet gravelly area (group A) can be identified in model 2. A second ridge occurs further from the river's edge where the soil is drier, very gravelly and sparsely vegetated (B). Model 2 also shows a small amount of (B) on the top of the first ridge. The hollow behind the first ridge is low and wet. Quadrat groups (A) and (D) occur in this zone, both possess damp soils; however, that of (D) is wetter and contains a higher clay and sand content than (A). In addition (D) is densely vegetated whereas (A) is not. Towards the rear of the gravel bank (i.e. behind the second ridge) vegetation increases probably by means of invading species from adjacent habitats. The soil of this group (E) is sandy and very dry. These five zones of vegetation (A to E) are readily recognized on most gravel banks.

Plants of P. pensylvanicum and P. lapathifolium were found in all groups of quadrats and this has been verified by field observations on many gravel banks. Large variations existed in dry weight values for these species within the groups which rendered most comparisons not significantly different upon analysis. The mean values per group showed trends that were different for each species. Within each species, only the smallest and largest mean dry weight values were significantly different ($P < 0.05$). P. pensylvanicum had greater dry weight values/m^2 for higher and drier parts of the gravel bank (the ridges and more

distant parts from the river's edge) than the lower and wetter areas. P. lapathifolium showed the opposite trend; the greater dry weight values/m^2 were obtained in the lower and wetter areas, namely on the river side slope of the first ridge and the hollow behind it (see Plate 4). This survey does not show whether the small size of plants of the study species was caused by competition with other species, by the habitat, or by both of these factors. The establishment experiments described in Chapter VI were designed to elucidate this problem. Field observations show that most of these small plants do reproduce, but the number of achenes produced is very low (often below 10/plant).

II.4 Discussion and conclusions

Reference material and distribution studies have indicated that there are differences in the types of habitats occupied by P. lapathifolium, P. pensylvanicum and P. persicaria.

P. lapathifolium has long been associated with man's agricultural activities and has probably increased its range with man's assistance to most of the temperature parts of the world. In southern Ontario, this species is probably not sufficiently abundant in cropland to be rated as a serious agricultural weed; it is more usually found in wet and naturally disturbed sites such as riverbanks, lake shores and exposed mud. In these habitats it is often

PLATE 4

Views of gravel bank 1 (see Survey IV, Chapt. II) showing the main distributions of large plants of Polygonum.

Upper: Dense vegetation (mainly of P. lapathifolium) on damp gravel at the river's edge.

Middle: Dense vegetation (mainly of P. lapathifolium) in hollows caused by vehicle tracks in the gravel bank.

Lower: Scattered large plants of P. pensylvanicum and Erysimum cheiranthoides on the dry gravel towards the rear of the gravel bank.

abundant even in more northerly sites in Ontario well away from agricultural land. On gravel banks in rivers, this species produces its greatest biomass in the lower and wetter hollows or right at the river's edge; however, its presence has been noted for all parts of this habitat.

P. pensylvanicum has a range that is more or less restricted to eastern North America and its northern limits are in southern Ontario. It is an agricultural weed throughout most of its range in the United States of America but in Canada it is generally restricted to the riverbanks and lakeshores in southern Ontario with the exception of Kent, Essex and Elgin counties in the extreme south west where it also occurs as a weed. On gravel banks of the Thames River, near London, it produces its greatest biomass on the higher and drier ridges or towards the rear of this habitat although its presence has been noted for all parts of the gravel bank. Climate distribution maps showed that various temperature parameters matched the distribution of P. pensylvanicum fairly closely. It may be speculated that its northern distribution is correlated with locations offering a mild climate and light warm soils such as those found on riverbanks and beaches.

P. persicaria, like P. lapathifolium, has long been associated with man's agricultural activities. It was with man's assistance that this species has become successfully established in North America from Eurasia. The two species will turn up or already occur in many areas not indicated

by the distribution maps in this chapter, as their ranges are probably still expanding. P. persicaria is particularly associated with damp clay soils supporting small grained cereal crops, such as oats, barley, rye and wheat. Farming practices and similar life cycles of the crops and weeds allow the persistence of this species with these crops. As a gravel bank species, P. persicaria was shown to be relatively rare compared with the preceding two species and it is possible that individuals found on gravel banks have been accidentally introduced by means of animal dispersal of the achenes or water run-off from fields washing them to the gravel banks. The list of species found on gravel banks 1, 2 and 3 (Appendix II.5) includes many that are more usually considered as weedy, woodland, marsh and even cultivated species, it appears that P. persicaria fits into this collection of species which are not confined solely to gravel banks. Poor survival of achenes in gravel bank soils (described in Chapter V) suggests that only by means of repeated introductions does this species maintain itself in this habitat. The distribution of P. persicaria in Ontario is restricted to regions of agricultural importance, it even occurs in isolated farming regions such as the clay belt and smaller farmed clay pockets in northern Ontario (Survey II, Chapter II).

Each species of Polygonum described here occurs in different habitats within the London area, P. lapathifolium

on the wetter parts of gravel banks, P. pensylvanicum on the drier parts of gravel banks and P. persicaria in damp farmland. The differences in habitat type mean that competition between individuals of two or more species is at a minimum. It can be theorized that in the past competition may have lead to the specific differences in habitat selection, especially between the native species P. lapathifolium and P. pensylvanicum. P. persicaria is native to Eurasia and presumably had already evolved its adaptations to man's agricultural methods before being introduced to North America.

CHAPTER III

WATER DISPERSAL OF ACHENES

III.1 Introduction

Efficient and long distance dispersal has been described as a characteristic of plants occurring in open and temporary habitats (Salisbury 1942). Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L. are abundant on the open gravel bars and banks of the Thames River, Ontario. This habitat is changed drastically by erosion, burial and flooding during winter months and severe droughts during the summer. Annual species growing in such a changeable habitat are dependent upon efficient dispersal for survival.

For riverbank species of Polygonum, dispersal away from the parent plant by floating and by animals (Chapter IV) has been reported by several workers. Dammer (1892), Guppy (1906), Praeger (1913), McAtee (1925) and Ridley (1930) have noted floating achenes of several species of Polygonum. In North Dakota, McAtee observed achenes of P. lapathifolium and P. persicaria washed up in lake debris and those of all three species in river debris. In addition, he saw a Redhead duck (Athya americana Eyton) feeding on floating achenes of P. lapathifolium.

Observations of the diaspores (dispersal units; van der Pijl 1969) in transit, have led to the inference

that many species of Polygonum are hydrochorous (water dispersed). Questions concerning hydrochory other than the buoyancy aspect have received little attention and yet are essential to the process. Such are:

1. Do the diaspores fall in microsites from which they can be dispersed by water?
2. Are the diaspores morphologically and physiologically suited to water transport?
3. How long do the diaspores remain buoyant? Previous work by Guppy, Praeger and Ridley is summarized in Table III.1.
4. Does hydrochory alter the dormancy or viability of the diaspores?
5. Are the diaspores deposited in sites suitable for subsequent germination and growth?

Questions 1 and 5, dealing with the presentation of the achenes to the dispersal agent and the deposition by the agent are examined in the section III.4. Problems relating to transport by the agent (questions 2, 3, 4) were investigated experimentally.

III.2 Methods and Materials

III.2.1 Achene sources

The achenes used in the experiments (Chapters III-VI) were gathered along the Thames River between Fanshawe Dam and the village of Muncey, Middlesex Co., Ontario (Fig. I.1). Inflorescences were shaken into collecting bags; this ensured

Table III.1 Duration of achene buoyancy (in days) as given by previous workers.

Species / Author	Guppy (1906)	Praeger (1913)	Ridley (1930)
P. lapathifolium	0 - 7	1	-
P. maculatum (synonym of P. lapathifolium)	-	3	-
P. pensylvanicum	-	-	-
P. persicaria	0 - 7	1	3

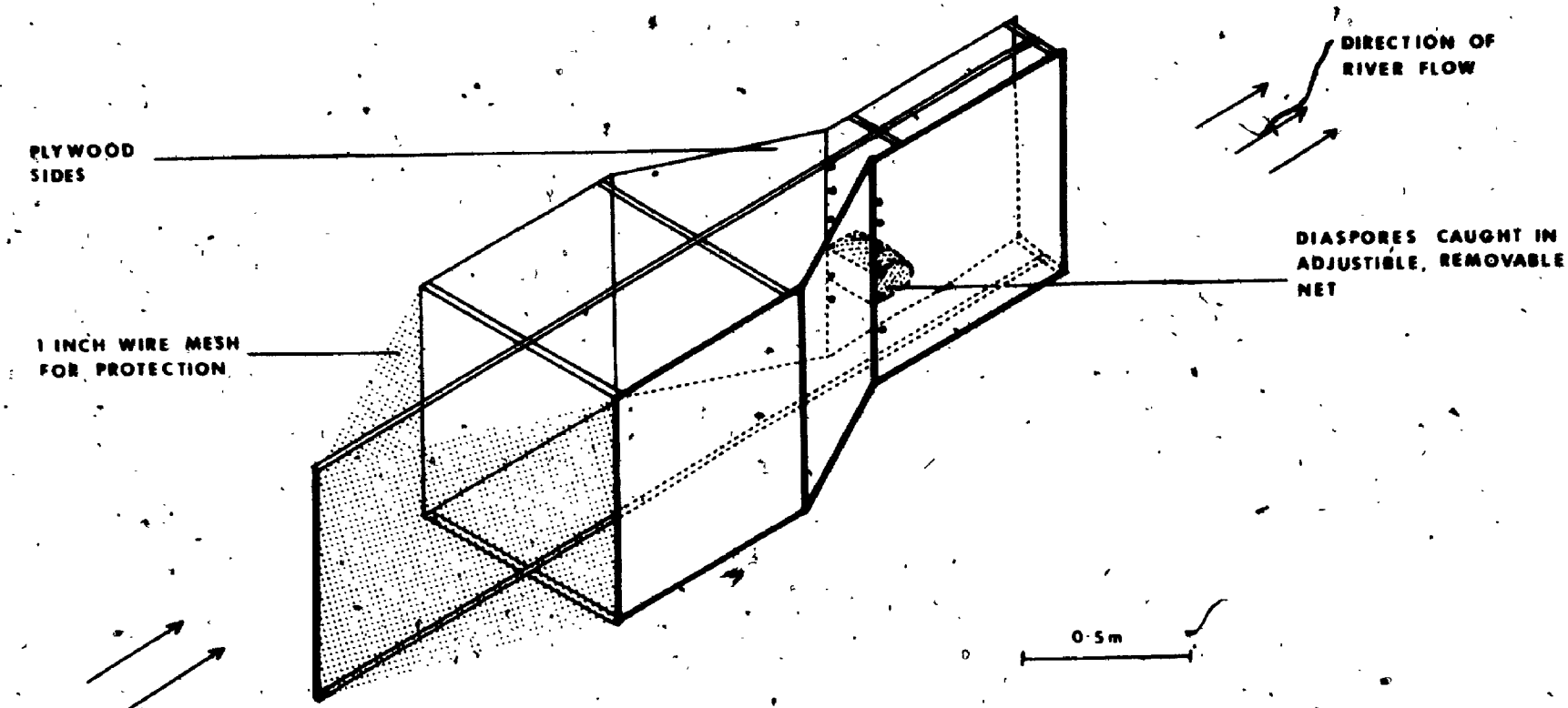
that only ripe achenes were collected. Usually the achenes were gathered on the day of the experiment. When the achenes were stored before use, the storage conditions are described under "Methods and Materials". A few experiments required achenes grown under known and controlled conditions, or at an unnatural season for fruiting. These were collected from plants grown in the greenhouse.

III.2.2 Experiment 1. Diaspore floatation in the Thames River

A diaspore trap was constructed (Fig. III.1) and anchored in the North Branch of the Thames River near its junction with Medway Creek in London (43°00'52.2"N 81°16'10.6"W) shown in Fig. I.1.

A fine nylon mesh caught any floating diaspores. This net was raised or lowered according to fluctuations in the water level. Another net caught any diaspores between 10 cm and 30 cm beneath the surface. The nets were emptied weekly and their contents placed in a cold (4°C) moist environment for 4 months to ensure that any stratification requirements had been met (see Chapter V). The flotsam was then placed in an incubator (14 hours, light 25°C/ 10 hours darkness, 10°C) for 2 months. Resulting seedlings were grown to maturity in the greenhouse to ensure correct identification. The diaspore trap was washed away during a storm in mid-December and data on spring dispersal are not available.

FIG. III.1 DIASPORE TRAP USED IN EXPERIMENT ONE.


PLYWOOD SIDES
1 INCH WIRE MESH FOR PROTECTION
DIRECTION OF RIVER FLOW
DIASPORES CAUGHT IN ADJUSTIBLE, REMOVABLE NET
0·5m

For the duration of this experiment, weekly precipitation was calculated from daily data issued by the London Weather Office at London Airport. Maximum weekly river depths above the summer minimum level were also recorded.

III.2.3a Experiment 2a. Duration of buoyancy for fresh, dry and overwintered diaspores

Achenes falling from the parent plants in autumn may be transported by the autumn or spring high water levels. At these times the diaspores would be fresh or overwintered respectively. Recently shed achenes on the soil surface may be subjected to considerable drying before transportation.

This experiment was planned to examine the duration of buoyancy of diaspores in three conditions (i.e. fresh, dry and overwintered). Buoyancy tests were run using diaspores with and without their perianths to assess the importance of the perianth to floating. See Section III.4.1.

The experiment commenced on March 31st, 1970. Plants had been grown in the greenhouse at various dates which made available fresh, dry and overwintered achenes simultaneously on this date. The 'fresh' achenes were gathered on the day of the experiment. The 'dry' achenes had been gathered 30 days earlier and left to air dry at room temperature until the start of the experiment. The 'overwintered' achenes had been gathered on February 15th, 1970 and placed in nylon bags which were pegged down on a gravel bar until March 31st, 1970.

The duration of buoyancy was determined in both still and agitated water. In both instances three replicates (100 diaspores per replicate) of each species/diaspore condition/perianth presence or absence combination were placed separately in 2 lb. glass jars, two-thirds full of distilled water. The experiments were conducted in the laboratory at a temperature of 23°C in natural light conditions. The numbers of floating diaspores in the still water were counted at weekly intervals for six months. The agitated treatment was achieved by placing the jars in an electrically operated shaker, adjusting the speed until maximum swell was accomplished with no splashing. The shaker was stopped momentarily for counting after 2, 4, 8, 18, 28, 38, 48, 58, 68 and 78 hrs. All diaspores in the agitated water had sunk within 84 hrs.

III.2.3b Experiment 2b. Diaspore dormancy and viability after 84 hrs. of agitation in water

After 84 hrs. of agitation, the dormancy and viability of the achenes were compared with those of a control set that had not been subjected to the buoyancy test. The controls consisted of three replicates (each of 100 diaspores) for each treatment combination described in Section III.2.3a. These achenes were placed on moistened filter papers in petri dishes for 84 hours, under the same conditions of light and temperature as the agitated achenes.

The germination test consisted of placing all the achenes on moist filter papers in petri dishes in an incubator (14 hours, light, 25°C/10 hours, darkness, 10°C) for 60 days by which time germination had terminated. Germinated achenes were counted daily and removed.

Ungerminated achenes were tested for viability by placing them in a cold (4°C) moist environment for six months and then replacing them in the 25°/10°C incubator for a further 30 days. Any achene which remained ungerminated after this additional treatment was recorded as inviable. In respect to the known requirements for dormancy breakage, this was considered to be an adequate test for viability. (See Chapter V)

III.3 Results

III.3.1 Experiment 1. Diaspores caught in the Thames River

Achenes of Polygonum lapathifolium, P. pensylvanicum and P. persicaria were caught in the diaspore trap from the surface of the North Branch of the Thames River. The numbers caught are given in Table III.2. No achenes were caught at 10-30 cm below the surface. The degrees of correlation of the numbers caught with the amount of precipitation, with the depth of the river and between species are given in Table III.3. The non-normal data were analysed using Spearman's rank correlation method (Sokal and Rohlf 1969).

Propagules of other species caught in the trap were; Ambrosia trifida L., Cirsium vulgare (Savi) Tenore,

Table III.2 Results of the diaspore trap experiment

Week ending	Number of diaspores caught per week			Weekly precipitation totals (cm.)	River depth (cm.)
	P. lapathifolium	*P. pensylvanicum*	*P. persicaria*		
1. 22- 9-71	60	12	1	2.4	18.8
2. 29- 9-71	18	0	0	0.8	18.5
3. 6-10-71	18	0	0	0.6	18.1
4. 13-10-71	51	15	9	2.5	21.2
5. 20-10-71	11	0	8	0.0	21.2
6. 27-10-71	32	7	0	0.8	20.4
7. 3-11-71	238	101	30	0.1	40.7
8. 10-11-71	161	90	25	0.4	46.8
9. 17-11-71	12	2	1	0.5	15.5
10. 24-11-71	17	12	0	1.5	16.7
11. 1-12-71	30	0	0	1.2	17.0
12. 8-12-71	21	17	0	1.5	15.2
Totals (12 wks.)	669	256	74		

Table III.3 Values of r_s (Spearman's Coefficient) for each pair of variables examined in Experiment 1 with their levels of significance. (n.s.) no significant correlation at the 5% level, (*) significant positive correlation at the 5% level, (**) significant positive correlation at the 1% level.

	a	b	c	d	e
a. Weekly achene numbers; *P. lapathifolium*	1.00				
b. Weekly achene numbers; *P. pensylvanicum*	0.67 *	1.00			
c. Weekly achene numbers; *P. persicaria*	0.46 n.s.	0.52 n.s.	1.00		
d. Weekly precipitation	0.16 n.s.	0.13 n.s.	0.38 n.s.	1.00	
e. River depth	0.58 *	0.29 n.s.	0.73 **	0.38 n.s.	1.00

Echinochloa crusgalli (L.) Beauv., Eragrostis pectinacea (Michx.) Nees, Leersia oryzoides (L.) Savi, Lemna minor L. (whole plants), Lythrum salicaria L., Muhlenbergia frondosa (Poiv.) Fern., Nasturtium officinale R. Br. (one branch), Polygonum hydropiper L., Rumex crispus L., Typha latifolia L. and Xanthium strumarium L.

III.3.2a Experiment 2a. Duration of achene buoyancy

Still water

Surface tension was important to achene buoyancy, except for the achenes with no perianths which had been overwintered. Achenes which had not sunk initially when placed on the water surface stayed afloat for six months, (Table III.4).

Between 75% and 99% of dry and fresh achenes with intact perianths remained afloat, the numbers of buoyant achenes slightly exceeded the numbers of fresh achenes for each species. Perianth removal in these two treatments reduced the numbers floating to between 28% and 61% after six months. Overwintered achenes with perianths showed between 15% and 38% buoyancy, those with no perianths showed no buoyancy. Apparently, during the overwintering process, the achenes had lost their ability to remain afloat, probably due to a change in the fruit wall. Analysis of information (see Appendix III.1) was applied to these data. The results are shown in Appendix III.2a.

Table III.4 Percentages of achenes afloat in still water after 6 months. The mean of three lots, each of 100 achenes is given for each treatment.

Achene condition		*P. lapathifolium*	*P. pensylvanicum*	*P. persicaria*
1. Fresh	- with perianth	75.3	91.7	88.0
	- no perianth	28.0	31.3	38.0
2. Dry	- with perianth	99.0	94.3	97.6
	- no perianth	61.3	33.0	40.3
3. Overwintered	- with perianth	38.3	27.3	15.0
	- no perianth	0.0	0.0	0.0

Agitated water

An information analysis was used to find differences in the floating ability of diaspores. Details of these calculations are given in Appendix III.1 and their results in Appendix III.2b. This analysis was applied to data gathered at 0, 2, 4, 8, 28, 48 and 68 hours and the results are illustrated in Figures III.2 to III.4.

A few of the dry and fresh achenes of each species remained afloat after 68 hours of agitation, indicating sufficient buoyancy to allow transport over considerable distances on the river.

Complete removal of the perianths resulted in the immediate sinking of at least 40% of the achenes and at least 90% after two hours of agitation. After overwintering outdoors the perianth segments had partly decayed, but buoyancy was still greater than for achenes from which the perianths had been removed ($P < 0.01$).

Diaspores of P. lapathifolium showed significantly ($P < 0.01$) greater buoyancy than those of P. pensylvanicum and P. persicaria. For the few times when the floating ability differed between P. pensylvanicum and P. persicaria, the latter showed greater buoyancy.

III.3.2b Experiment 2b. Germination and viability

Although counts were made for 60 days, no germination occurred after 30 days. Figures III.5 to III.7 show the cumulative germination curves for each species/achene condition/

FIG. III.2 BUOYANCY OF ACHENES OF P. LAPATHIFOLIUM IN AGITATED WATER. Solid line indicates achenes with perianth and broken line indicates achenes without perianth.

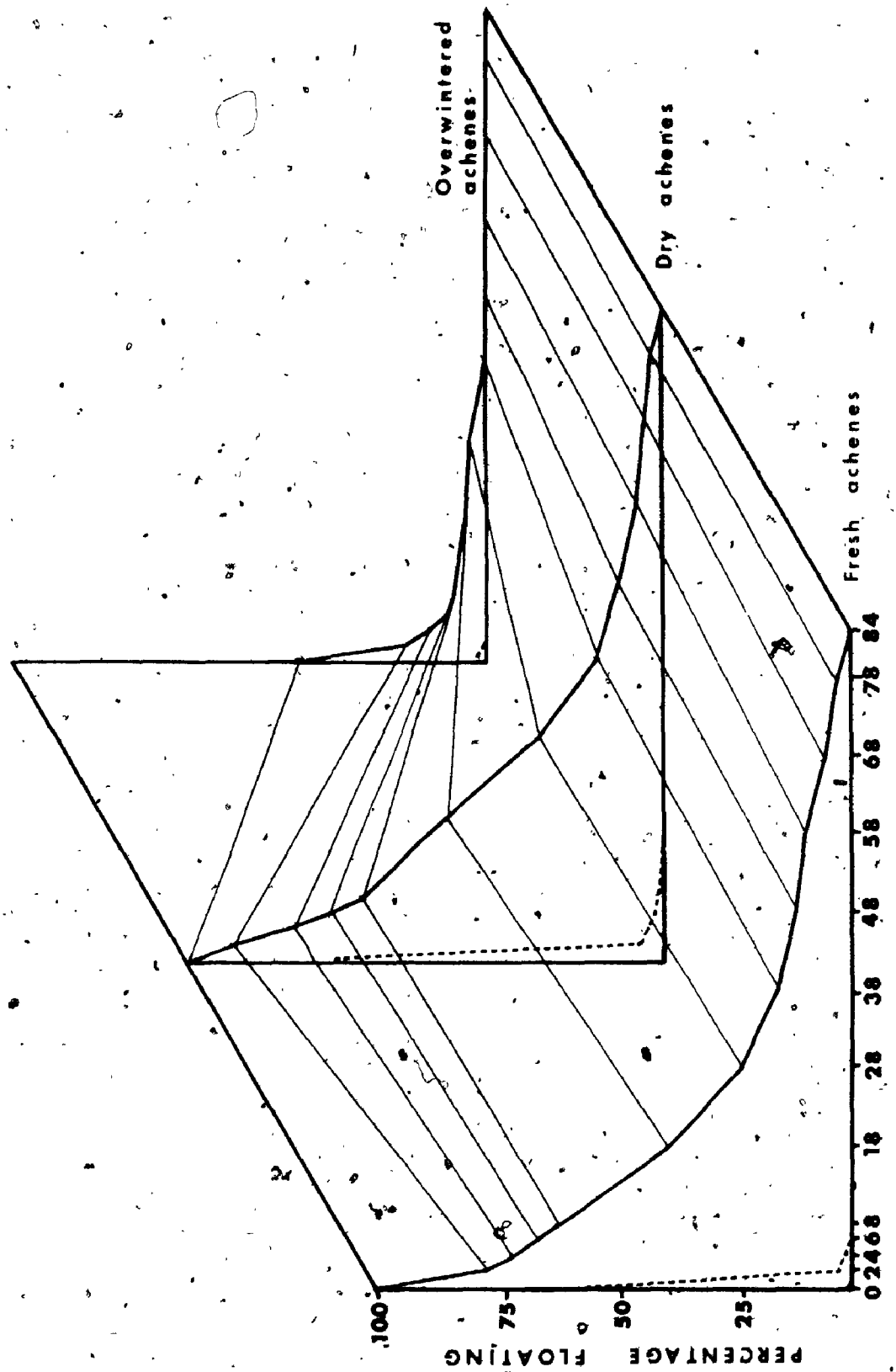

Overwintered achenes
Dry achenes
Fresh achenes
PERCENTAGE FLOATING
100
75
50
25
0
2
4
6
8
18
28
38
48
58
68
78
84
TIME IN HOURS

FIG. III.3 BUOYANCY OF ACHENES OF P. PENSYLVANICUM IN AGITATED WATER. Solid line indicates achenes with perianth and broken line indicates achenes without perianth.

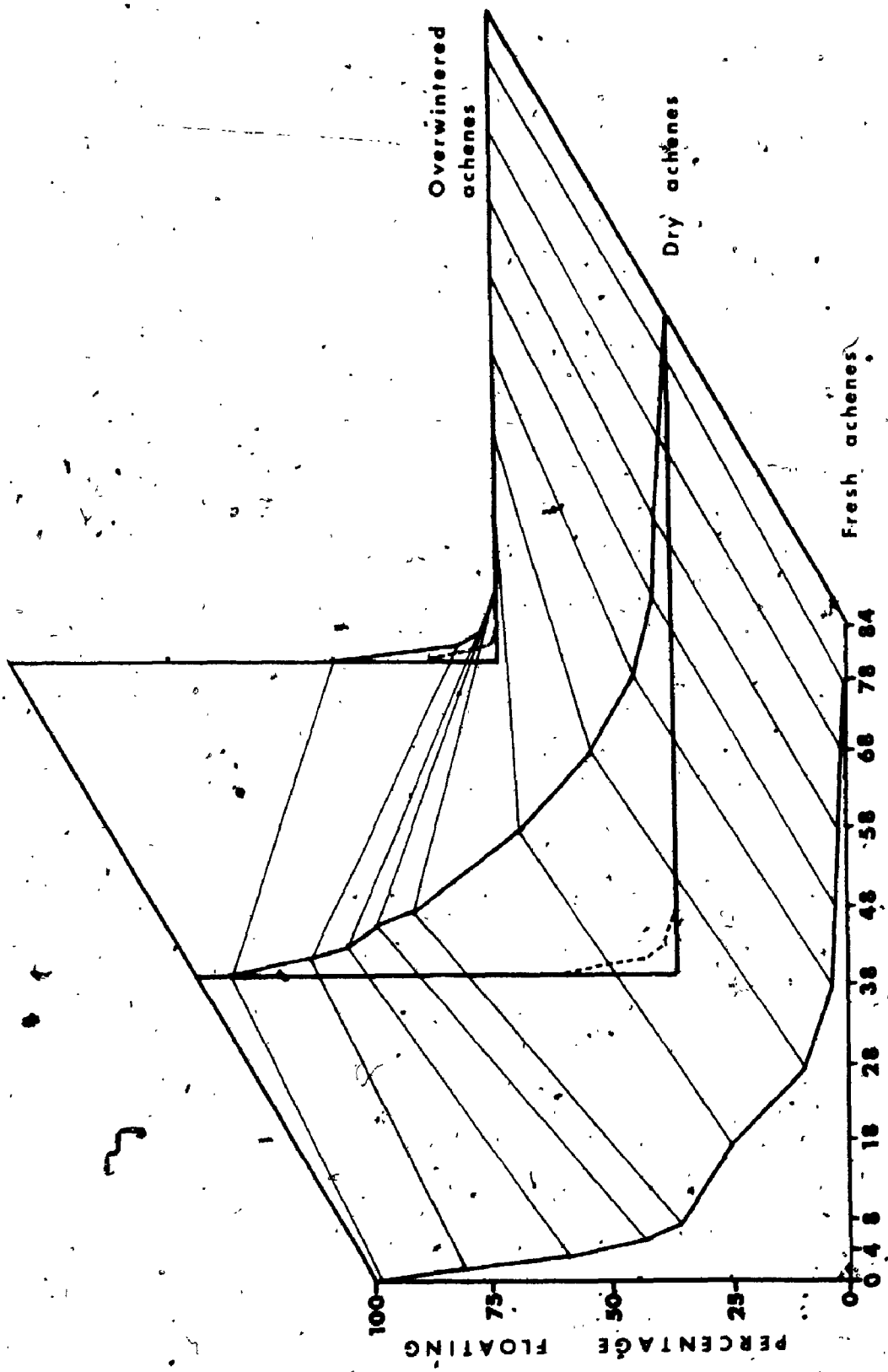

Overwintered achenes
Dry achenes
Fresh achenes
PERCENTAGE FLOATING
100
75
50
25
0
0 4 8 18 28 38 48 58 68 78 84
TIME IN HOURS

FIG. III.4 BUOYANCY OF ACHENES OF P. PERSICARIA IN AGITATED WATER. Solid line indicates achenes with perianth and broken line indicates achenes without perianth.

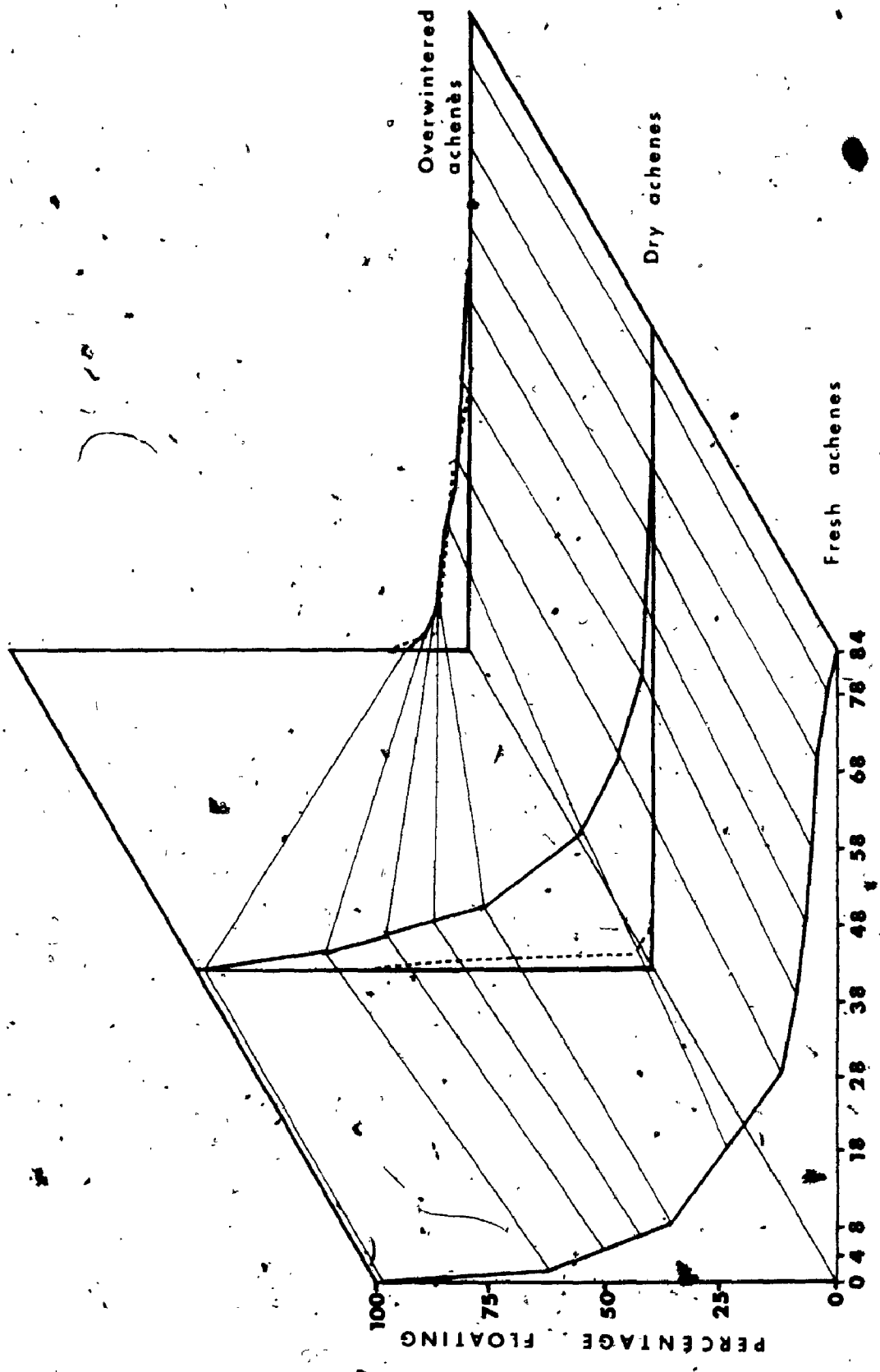

Overwintered achenes
Dry achenes
Fresh achenes
PERCENTAGE FLOATING
100
75
50
25
0
0 4 8 18 28 38 48 58 68 78 84
TIME IN HOURS

FIG. III.5 GERMINATION OF ACHENES OF P. LAPATHIFOLIUM AFTER BUOYANCY TESTS. Solid line indicates achenes previously agitated in water. Broken line indicates achenes from non-agitated water. S indicates significantly different germination totals ($P < 0.05$).

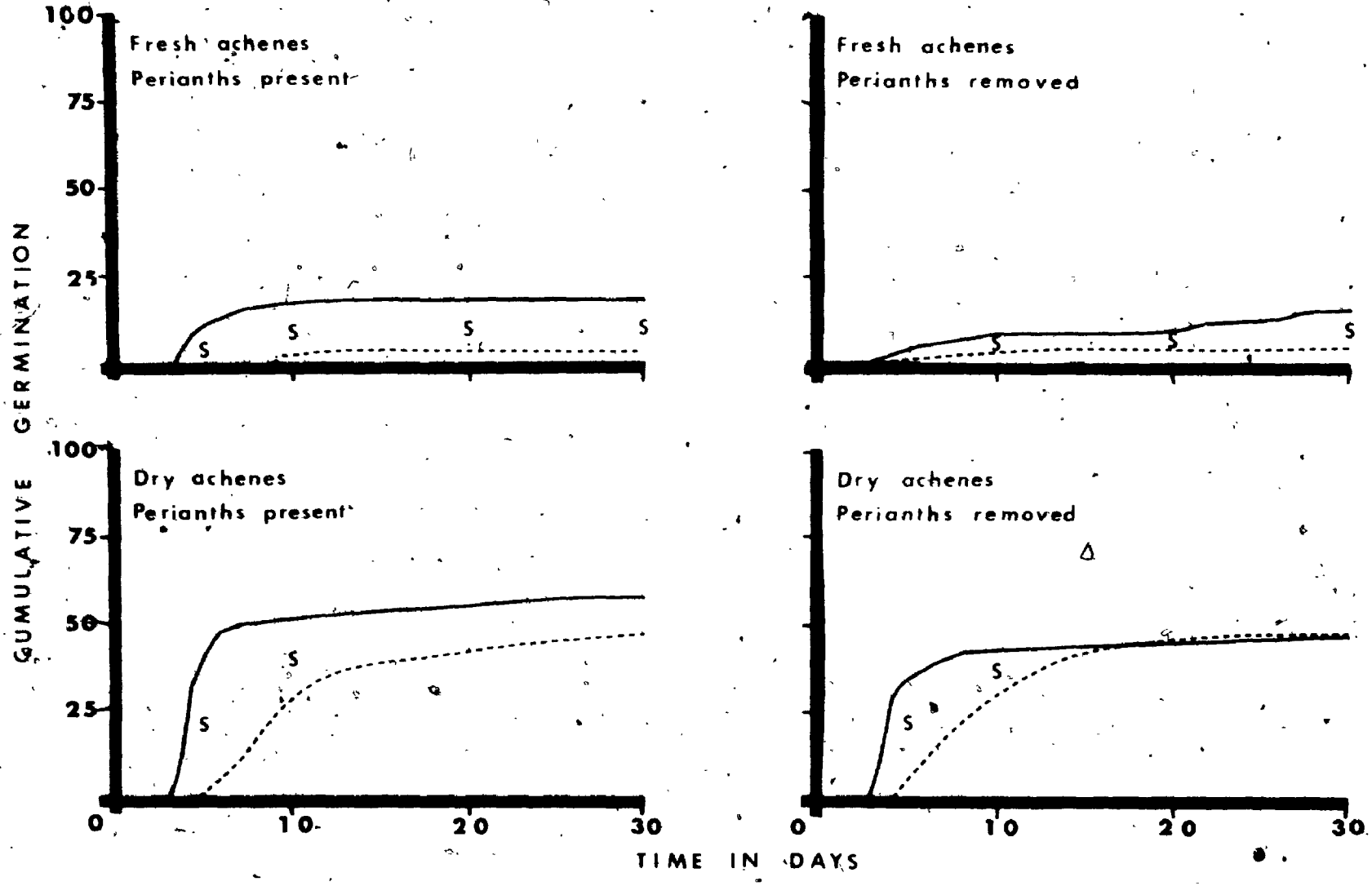

Fresh achenes
Perianths present
Fresh achenes
Perianths removed
Dry achenes
Perianths present
Dry achenes
Perianths removed
100
75
50
25
0
10
20
30
S
CUMULATIVE GERMINATION
TIME IN DAYS

FIG. III.6 GERMINATION OF ACHENES OF P. LAPATHIFOLIUM AND P. PENSYLVANICUM AFTER BUOYANCY TESTS. Solid line indicates achenes previously agitated in water. Broken line indicates achenes from non-agitated water. S indicates significantly different germination totals ($P < 0.05$).

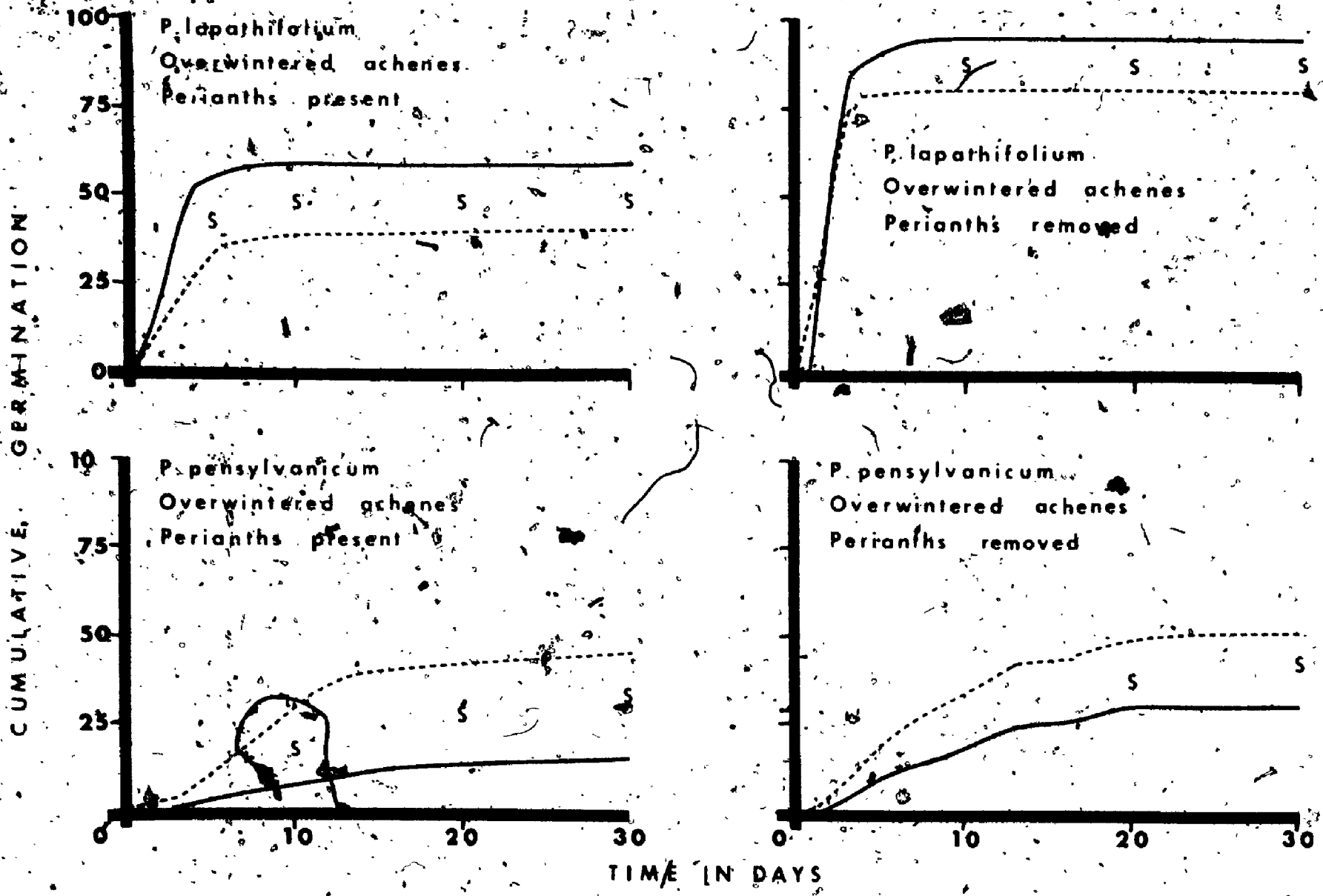
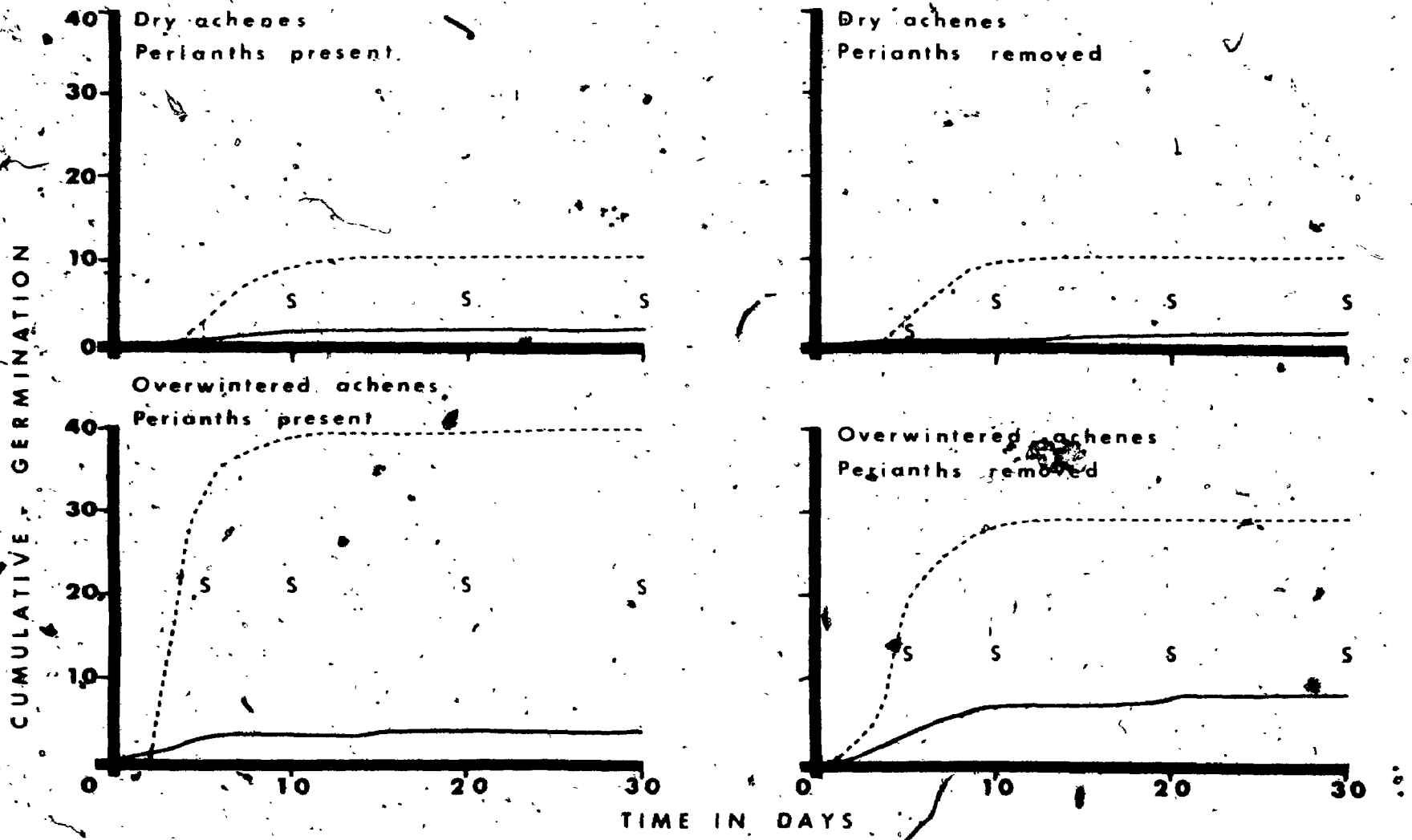

P. lapathifolium
Overwintered achenes
Perianths present
P. lapathifolium
Overwintered achenes
Perianths removed
P. pensylvanicum
Overwintered achenes
Perianths present
P. pensylvanicum
Overwintered achenes
Perianths removed
S
100
75
50
25
0
10
20
30
CUMULATIVE GERMINATION
TIME IN DAYS

FIG. III.7 GERMINATION OF ACHENES OF P. PERSICARIA AFTER BUOYANCY TESTS. Solid line indicates achenes previously agitated in water. Broken line indicates achenes from non-agitated water. S indicates significantly different germination totals ($P < 0.05$).


Dry achenes
Perianths present
Dry achenes
Perianths removed
Overwintered achenes
Perianths present
Overwintered achenes
Perianths removed
CUMULATIVE GERMINATION
TIME IN DAYS
0
10
20
30
40
S

perianth presence or absence combination. Viable achenes were considered dormant if they had not germinated by this time.

Comparisons were made between germination scores (5, 10, 20, 30 days) of the agitated achenes and the non-agitated controls using information statistic. Details of results are shown in Appendix III.3.

Water agitation caused significant changes in subsequent germination (except P. lapathifolium dry, no perianth). In P. pensylvanicum and P. persicaria agitation decreased subsequent germination percentages. In P. lapathifolium, for fresh, dry and overwintered treatments germination was increased by previous agitation in water.

Germination patterns between species, treatments and controls varied little. Two noteworthy exceptions occurred. Firstly, all overwintered achene treatments commenced germination within three days of being placed in the incubator, whereas the other treatments took longer. Secondly, achenes of P. pensylvanicum germinated over a longer period of time than those of the other two species.

Preliminary experiments showed that greenhouse grown achenes (as used in this experiment) did not differ in germination results from those collected along the river banks.

Achene viability

Stratification of dormant achenes, followed by a second germination test boosted germination totals to at

least 99% for all treatment combinations. The few achenes still ungerminated were dissected and found to be rotten. Agitation in water for 84 hours, therefore, had no significant effect on viability of achenes of P. lapathifolium, P. pensylvanicum or P. persicaria.

III.4 Discussion and conclusions

The three stages of water dispersal were examined by means of experiments and observations. The stages were; presentation of the diaspore to the dispersal agent, transport by the agent and deposition by the agent. Success during each stage depended on 1) the completion of that stage and 2) any physiological changes occurring in the diaspore being favourable to eventual success in dispersal.

III.4.1 The achene as a hydrochorous diaspore

The achene is the only dispersal and overwintering unit in P. lapathifolium, P. pensylvanicum and P. persicaria. Achenes are dry, indehiscent, one-seeded fruits. In shape they are usually lenticular for all three species, however, they are occasionally trigonous in P. persicaria and rarely trigonous in P. lapathifolium. The achenes of each species possess shiny, thick hard coats consisting of the heavily cutinised epidermal layer and the compressed inner layers of the ovary (Sirrine 1895). Mean achene lengths, widths and weights have been calculated for each species and given in Table III.5.

The mature achene is enclosed by a persistant and tightly appressed perianth. At pre-anthesis and early

Table III.5 Achene sizes and weights. (Means and standard errors.)

	Length (mm.) (Based on 100 achenes per species)	Width (mm.)	Weights (g.) per 100 achenes[1]		
			fresh[2]	dry[2]	overwintered[2]
P. lapathifolium	1.93 ± 0.02	1.68 ± 0.02	0.1901 ± 0.0038	0.1449 ± 0.0031	0.2065 ± 0.0042
P. pensylvanicum	3.05 ± 0.02	2.92 ± 0.03	0.6537 ± 0.0032	0.4693 ± 0.0026	0.7142 ± 0.0025
P. persicaria	2.26 ± 0.01	1.66 ± 0.02	0.2410 ± 0.0012	0.1621 ± 0.0017	0.2688 ± 0.0020

1 Means and standard errors for achene weights were based on three lots of 100 achenes per species weighed with the perianth segments attached.

2 "Fresh achenes" were weighed on the day of collection.
"Dry achenes" were allowed to dry at room temperature for 1 month.
"Overwintered achenes" were stored outside on the ground surface for 6 weeks.

post-anthesis the perianth segments are loosely arranged and possess large fluid-filled cells. As the achene matures, the cells dry and the segments contract. During this process they become imbricate and tightly wrapped around the achene. Air spaces remaining between the achene and the perianth give the diaspore buoyancy. The perianth of P. lapathifolium is extended as an air-filled "beak" over the remains of the stigma (Moss 1914).

During the winter the perianth decays and is partially or completely absent by the following spring. P. lapathifolium differs from the other species in that the outer perianth segments possess anchor shaped veins which persist long after the remainder of the perianth has decayed (see Fig. III.8).

In the form of a dormant achene, the individual Polygonum plant is in a convenient state for both survival during severe environmental conditions and for dispersal.

III.4.2 Presentation of the diaspores to the dispersal agent

In the area studied, the plants grow from the water's edge to a distance of 30 m from it.

Achenes reach maturity and fall from the parent plant between the end of July and the beginning of November. The main achene dehiscence times differ between species; P. persicaria, August; P. lapathifolium, mid-September and P. pensylvanicum, late September to early October. Some

FIG. III.8 ACHENES AND PERIANTHS OF POLYGONUM SPP.

ROWS (SPECIES): a) P. lapathifolium

b) P. pensylvanicum

c) P. persicaria

COLUMNS (ACHENE AND PERIANTH CONDITIONS):

i) fresh

ii) dry

iii) overwintered

iv) perianths removed

1 mm.
iv)
iii)
ii)
i)
a)
b)
c)

achenes within a spike mature while adjacent flowers have not reached anthesis, therefore shattering is prolonged for any one spike. The perianth segments are not extended as wings to assist in wind dispersal as they are in P. scandens L. and some other species. After shattering, most diaspores are, therefore, restricted to an area beneath the parent plant. Some diaspores, especially the smaller ones (P. lapathifolium and P. persicaria) fall into the interstices of the gravelly substrate and are not readily dispersed, instead they become part of the dormant buried seed population. Some plants grow sufficiently close to the water's edge that the diaspores drop directly into the water (see Plate 5); however, large numbers of achenes fall first onto the surface of the substrate.

The pale gravel surface reflects much heat (Lubke 1968), causing achenes lying upon it to become very dry. The degree to which the achenes and perianth segments dry influences the subsequent duration of buoyancy. Drying depends on two factors, firstly, the duration between the time of shattering (see above) and dispersal and secondly, upon the weather conditions during this duration.

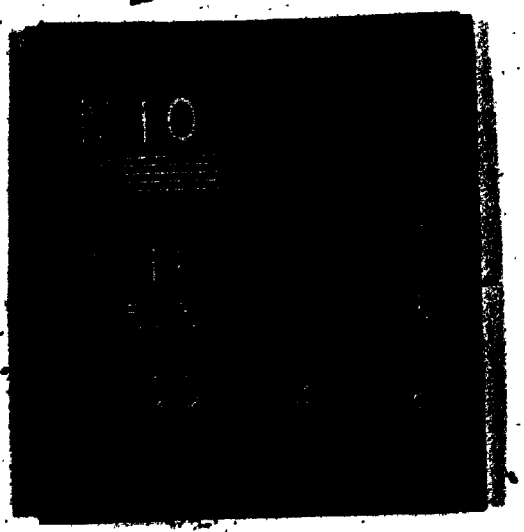
The parent plants usually grow below the high water level. Autumn fluctuations in this level caused achenes to be floated away from the riverbank. The effects of rain washing diaspores into the river were not important.

PLATE 5

Photograph showing aspects of hydrochory. Buoyant achenes can be seen on the surface of the water immediately beneath overhanging, pendulous, fruiting spikes of a large plant of P. lapathifolium.

35

OF/DE



III.4.3 Transportation of the diaspores by the dispersal agent

Diaspores of P. lapathifolium, P. pensylvanicum and P. persicaria were caught by means of a diaspore trap (experiment 1). The proportions of diaspores caught were P. lapathifolium, 9: P. pensylvanicum, 3.5: P. persicaria, 1. These differences between species are the results of several influencing factors; the relative numbers of plants along the water's edge (lowest for P. persicaria), the positions occupied on the riverbank, the numbers of diaspores produced per plant (lowest in P. persicaria), the success of presentation of the diaspores to the agent and the duration of buoyancy (shortest in P. pensylvanicum).

The duration of buoyancy depends on the length of time that the density of the propagule is less than that of water and ends by its sinking or beaching. Extremely long buoyancy can be disadvantageous as the diaspore could end its floating stage in salt water.

Cavers and Harper (1964) have shown that propagule buoyancy in the maritime variety of Rumex crispus L. (family; Polygonaceae) is almost entirely due to persistent perianth segments which possess corky tubercle-like appendages.

The duration of achene buoyancy in the three species of Polygonum varied from 0 hours to at least 6 months according to species, presence of the perianth, storage

conditions of the achenes and whether the water was agitated.

Achenes of P. lapathifolium floated for the longest duration while those of P. pensylvanicum sank earliest. This sequence of species also reflects increasing achene size and weight from P. lapathifolium to P. pensylvanicum (see Table III.5). The air-filled perianth "beak" in P. lapathifolium undoubtably increased buoyancy in that species.

In agitated water, perianth presence was essential to floatation for long periods, regardless of species. Without perianths, these achenes floated for approximately 2 hours whereas those with perianths showed floatation for up to 60 hours. The results of buoyancy tests conducted by Praeger, Ridley and Guppy (Table III.1) are comparable with these results for achenes with perianths attached. In still water, achenes with perianths were again more buoyant, however, water surface tension increased the buoyancy for all achenes. On rare occasions it has been observed that the perianth segments have been partly eaten by unknown herbivorous animals. This would considerably reduce the duration of buoyancy for these achenes.

Duration of buoyancy was only marginally greater for dry stored achenes than fresh achenes. Achenes of P. persicaria and P. lapathifolium ripen earlier than do those of P. pensylvanicum and would dry more thoroughly before transportation by autumn floods. Perianths of

overwintered achenes were partly decayed and afforded little buoyancy in agitated water; however, the duration of buoyancy was greater than for achenes from which the perianths had been completely removed. These low values suggest that water dispersal in spring floods is very limited, especially as the period of overwintering was much shorter in the experiment than in nature. Overwintered achenes without perianths differed from achenes of other storage conditions in sinking in still water. The overwintering process probably altered the structure of the fruit wall and thus prevented floatation due to water tension.

Buoyancy in still water exceeded that in agitated water for all species, perianth and achene conditions. This was attributed to two reasons. Firstly, air spaces within the perianth segments quickly become waterlogged in agitated water, and secondly, water tension was weak in agitated water.

Water agitation influenced subsequent germination totals (increase in P. lapathifolium, decrease in P. pensylvanicum and P. persicaria). These interspecific differences show different germination strategies. Achenes of P. lapathifolium would tend to germinate in the autumn after water dispersal, those of the other two species would be inhibited from germinating until the following spring. Autumn germination of achenes produces plants which only survive under exceptionally mild autumns and if the river water levels remained low. Water agitation for 84 hours did not alter the viability of achenes.

III.4.4 Deposition of the diaspores by the dispersal agent

The transport stage of water dispersal usually ends with sinking or beaching of the diaspore. No diaspores were caught in the trap between 10 cm and 30 cm below the water surface suggesting that the achenes sink quickly once buoyancy is lost. Decay of the perianth segments and exposure of the flat achene would minimize rolling on the river bed unless the currents were strong. The anchor shaped perianth veins in P. lapathifolium (Fig. III.8) would tend to become entangled in other obstacles, thus fixing the diaspore in one place and assisting in subsequent establishment of seedlings. Such hooked anchorage devices are found in many hydrochorous species (van der Pijl 1969). Submerged diaspores were dormant until brought above the water surface and then if the temperature and moisture conditions were favourable, germination occurred quickly (see Chapter V). The diaspores did not show significantly reduced viability after a two year submergence (Chapter V). The longevity of achenes of P. hydropiper L. when stored in the soil is up to 60 years (Darlington and Steinbauer 1961). The drying out of the Speed River, Guelph, Ontario in 1963 resulted in the rapid emergence of seedlings of many hydrochorous species, including P. lapathifolium and P. persicaria (Dale 1964) on the river bed.

Beaching of diaspores has been witnessed by McAtee (1925) on the banks of lakes and rivers in North Dakota.

This would normally occur at the high water mark, a place at which the species are frequently abundant (Chapter II).

CHAPTER IV

DISPERSAL OF ACHENES BY COTTONTAILS

IV.1 Introduction

During the autumns of 1968 to 1971 a list was made of the animal visitors to large, mixed stands of Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L. (smartweeds) growing on riverbanks. Cottontail rabbits (Sylvilagus floridanus Allen) were frequently seen feeding on these plants; closer examination revealed that they were eating ripe achenes. Cottontail faeces containing whole and fragmented achenes were abundant near the plants (Plate 6).

Many bird and mammal species have been reported to eat smartweed achenes (Ridley 1930; Martin et al 1951, etc.). These reports suggest that the propagules are potentially endozoochorous (i.e. eaten, transported and excreted in a viable state by animals; van der Pijl 1969). Adaptations by higher plants to endozoochory have received few investigations.

My observations of cottontails feeding on smartweed achenes presented an opportunity for studying endozoochory more thoroughly. The following four experiments investigate 1) the occurrence of viable propagules of any species in field-collected faeces and the relative abundance of that species in the collecting area, 2) the length of time that whole and fragmented achenes are retained before excretion,

PLATE 6

Photographs showing aspects of endozoochory.

Upper: Large plants of P. lapathifolium from which achenes have been stripped for food by cottontails. Faecal pellets can be seen beneath the plants, these contained viable seeds of many species, including Polygonum.

Lower: Seedlings germinated in the greenhouse from faecal pellets collected at the site shown above.

L. left: Seedlings of P. lapathifolium (taller of the two) and Solanum dulcamara.

L. right: Seedlings of P. lapathifolium (taller of the two) and P. persicaria.

3) the percentage viability of achenes after excretion and 4) the percentage viability within different achene size groups after excretion. Experiment 3 and 4 utilized achenes of the three species mentioned above.

IV.2 Methods and Materials

IV.2.1 Experiment 1. Identification of viable propagules in cottontail faeces and abundance of plant species in the faeces collection area

In November 1970, cottontail faeces were collected from a gravel bar on the North Branch of the Thames River, London (43°00'52.2"N 81°16'10.6"W; see Fig. I.1). They were placed in nylon mesh bags and left on bare ground over winter; this ensured that any stratification requirements of viable propagules were met. (Stratification requirements in Polygonum are discussed in Chapter V). In early April 1971, faecal pellets were treated in four ways: 1) left intact outside, 2) left intact in the greenhouse, 3) broken up and placed in the greenhouse and 4) broken up, washed and placed in the greenhouse. Each treatment simulated a condition which could occur in the field and may have been of importance to the germination of any propagules within the faecal pellets. All pellets were placed on the surface of sterilized soil in seed flats (50 pellets/flat). Two hundred pellets (4 flats) were used in each treatment. The flats were enclosed in semi-transparent, fine gauze to prevent the introduction of extraneous propagules. As a control, two flats without pellets were included in each

treatment. In the greenhouse, the flats were watered daily and the temperature maintained at 18 ± 3°C. during the day and 24 ± 3°C. during the night. Each resulting seedling was grown to a size which allowed accurate identification. The numbers of each species were recorded.

Frequencies were determined for all plant species present at the faeces collection site, at the time of collection. A square area, 20 by 20 m centred at the point of collection was divided into 1 m square units. Lists of species were made for each of 25 randomly selected units.

IV.2.2 Experiment 2: The length of time that smartweed achenes were retained in the digestive tracts of captive cottontails.

During November and December 1970 and January 1971, seven cottontails were live-trapped on the riverbank where smartweeds had been grazed. During captivity the animals were provided with water; commercial rabbit food pellets ("Master Rabbit Food Pellets"; Purina Chow) and fresh green herbage (foliage of Taraxacum officinale Weber and Senecio officinalis L.). The cottontails were allowed at least one month to adjust to captivity before experiments were conducted.

The achenes used in this experiment were collected on the day of the experiment (see Section III.2.1). The perianths were left intact, but no smartweed foliage was provided as food.

A five gram lot of achenes of P. lapathifolium was given to each of three cottontails at 6 p.m. on the day of the experiment. At this time, all faecal pellets present in the cages were removed, the lights were extinguished and feeding commenced. After two hours, uneaten achenes were removed. Faeces were collected at 0, 2, 4, 8, 12, 24, 48 and 60 hours after the feeding period. This experiment was then repeated using achenes of P. persicaria. Achenes of P. pensylvanicum were not used in this experiment since Experiment 1 had shown that these achenes were too large to survive the mastication. (This finding was substantiated by later experiments).

Soaking the faecal pellets overnight, breaking them up by hand and centrifugation enabled intact achenes and fruit wall fragments to be extracted. The fragments and achenes were separated from each other, air dried and weighed.

IV.2.3 Experiment 3. The percentage viability of achenes after excretion by captive cottontails

Each of four cottontails was provided with four hundred achenes of one of the smartweed species. (For a discussion of the achene collection technique see Section III.2.1). All faecal pellets were removed from the cages at this time. Uneaten achenes were removed after twelve hours and counted. Fresh faeces were collected two days after the twelve hour feeding period. The experiment was repeated using achenes of the other species with five day intervals between successive feedings. Once collected, the

pellets were soaked overnight, broken up by hand, sieved (mesh diam, 0.71 mm) and the extracted achenes placed in a cold, moist (4°C) environment for four months to break dormancy. The total number of viable achenes in each of the four lots of four hundred was recorded for each of the three species.

IV.2.4 Experiment 4. Viability in achenes of different sizes after excretion by captive cottontails

A bulk sample of fresh, ripe achenes was collected as described in Section III.2.1. The achenes, with perianths removed were sieved into three size categories for each species. Mesh sizes used were 1.19 mm and 1.41 mm (for P. persicaria and P. lapathifolium) and 2.00 mm and 2.38 mm (for P. pensylvanicum). On the basis of 1000 achene weights, an estimation was made of the proportions of achenes in each size category for each species.

Twelve hundred achenes (3 lots of 400) per achene size/species combination were used in this experiment. Faeces were removed from the cages of six cottontails, and each was provided with one lot of achenes. Uneaten achenes were removed twelve hours later and counted. Faeces were removed two days after the feeding period. This procedure was repeated with five day intervals between successive achene feedings until each achene lot had been presented to a cottontail. The numbers of viable achenes from each size category were recorded for each species. (See Experiment 3 for viability tests.)

IV.3 Results

IV.3.1 Experiment 1. Propagules in field collected faeces

Germination in all test flats had finished by the end of July 1971. At this time no ungerminated entire smartweed achenes could be found in the faecal remains. Thirteen species germinated from the faeces (see Table IV.1), each is represented by a specimen in the herbarium of the University of Western Ontario (UWO). The species with the largest number of seedlings was Solanum dulcamara L. (65% of the total). Seedlings of P. lapathifolium were the second most abundant (25%) while those of P. persicaria were rare (1%). No seedlings of P. pensylvanicum occurred although many achene fragments of this species were present in the faeces.

One hundred and ten species of angiosperm plants were recorded from the faeces collection site. The frequencies recorded for species which had viable propagules in the faeces are shown in Table IV.1; the frequencies for all other species are given in Appendix IV.1. All species germinating from the faeces occurred at the collection site.

IV.3.2 Experiment 2. Retention times by captive cottontails

Few achenes remained after the two hour feeding period (P. lapathifolium, 0.27 gm.; P. persicaria, 0.32 gm.). Fig. IV.1 and Appendix IV.2 show the numbers of whole achenes and the amounts of achene fragments excreted for each hour during and after the feeding period. "Fragmented achenes" primarily consisted of fruit wall material; endosperm and

Table IV.1 The numbers of seedlings which emerged from field collected, cottontail faeces. (200 faecal pellets per germination condition)

Species	Germination conditions				Species totals	% frequency in vicinity of faeces
	outdoors intact	greenhouse intact	greenhouse fragmented	greenhouse leached		
Polygonum lapathifolium	18	14	8	3	43	96
P. persicaria	2				2	16
P. pensylvanicum					0	92
Solanum dulcamara	20	23	28	41	112	8
Plantago rugelii			3		3	8
Agrostis stolonifera		1	1		2	80
Barbarea vulgaris	1			1	2	64
Stellaria media			2		2	56
Chenopodium album		1			1	40
Digitaria ischaemum		1			1	4
Leersia oryzoides		1			1	84
Lythrum salicaria				1	1	80
Muhlenbergia frondosa		1			1	92
Plantago major				1	1	92
Germination condition totals.	41	42	42	47	172	

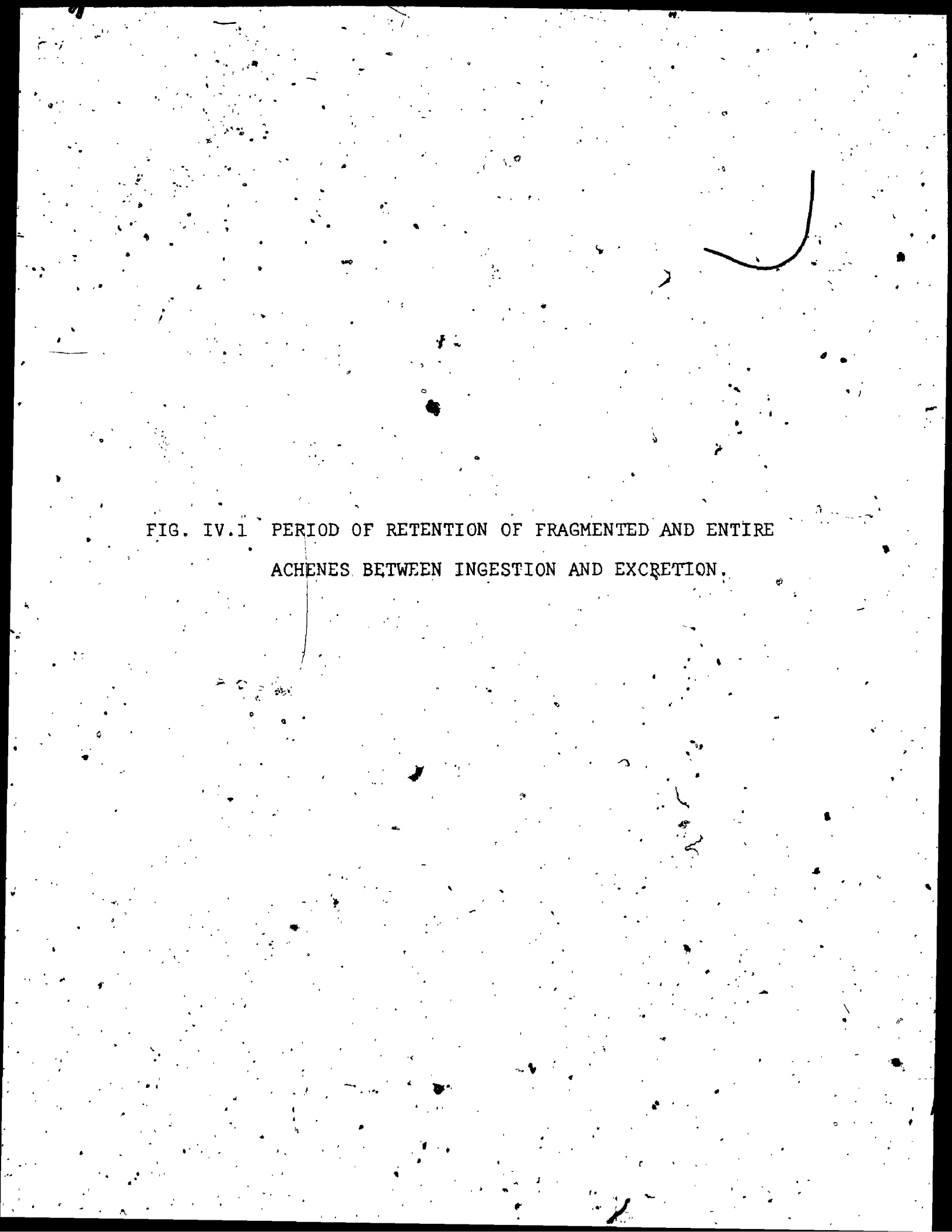
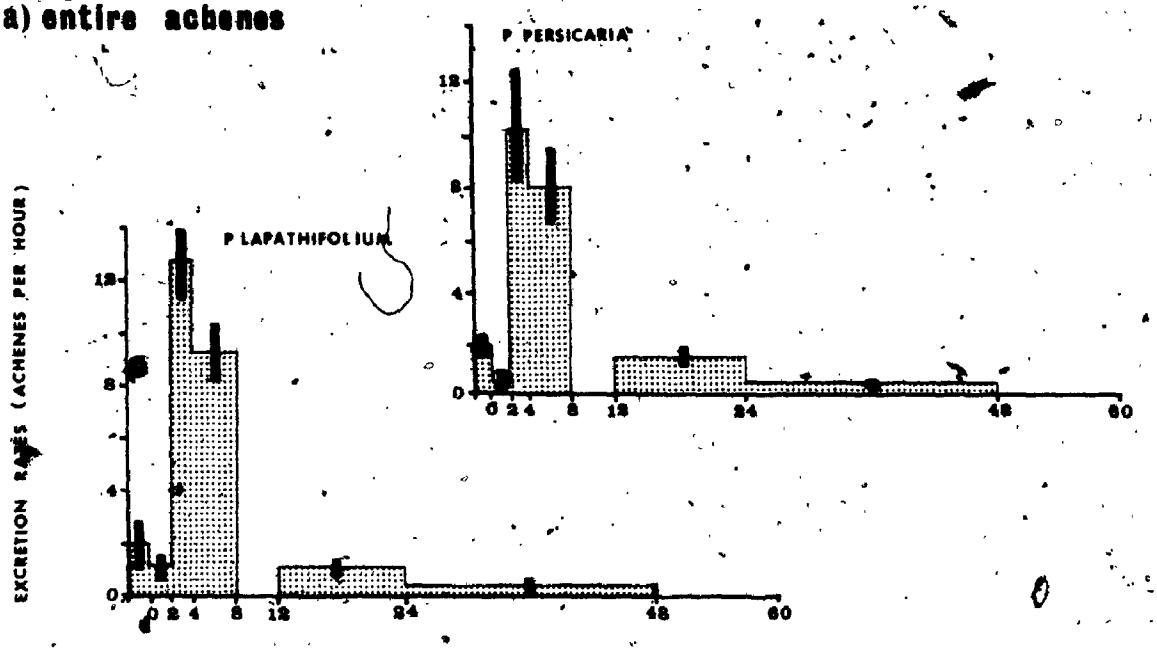
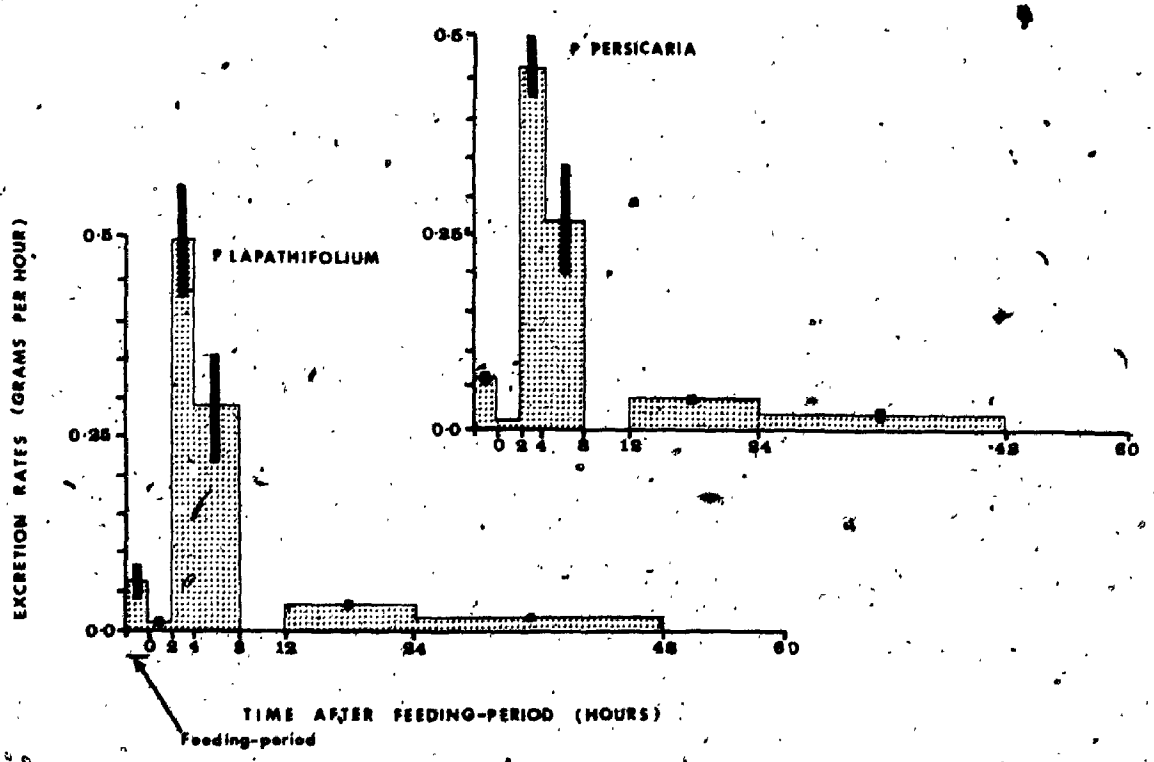


FIG. IV.1 PERIOD OF RETENTION OF FRAGMENTED AND ENTIRE ACHENES BETWEEN INGESTION AND EXCRETION.

a) entire achenes



b) fragmented achenes



embryonic tissues normally having been digested. The histograms represent mean values based on three replicates. Standard errors are given for each time period. Achenes were excreted up to 48 hours after the end of the feeding period. A peak occurred between 2 and 8 hours which was preceded and followed by periods of limited defaecation.

IV.3.3 Experiment 3. Viability of achenes after excretion

Information analysis was used in all comparisons of scores in this experiment; detailed results are given in Appendix IV.3. This method of analysis is described in Appendix III.1.

Some achenes from each lot of 400 were missed by the cottontails. These had been left around the edge of the feeding container or flicked out of it and lost through the wire mesh floor of the cage. These achenes were considered in the calculations of percentages viability. No significant differences existed between species regarding the numbers of achenes eaten.

The numbers of viable achenes after passage through digestive tracts of captive cottontails are shown in Table IV.2. Percentage values were too small to allow a sound analysis to be undertaken (Sokal & Rohlf 1969, pg. 565); however, comparisons were made between the actual numbers of viable achenes excreted. The total value for P. lapathifolium (67.00) was found to be significantly greater ($P < 0.01$) than that of P. persicaria (31.00). All recovered achenes of P. pensylvanicum were inviable.

Table IV.2 Results of Experiment 3, where smartweed achenes were fed to captive cottontails.

Each value is the total from four replicates. Values in the same column and followed by the same letter are not significantly different at the 5% level.

	Number of achenes provided to cottontails	Total number of achenes eaten	Total number of viable achenes after excretion	Mean percentage achene viability
P. lapathifolium	1600	1498[a]	67[c]	4.37
P. pensylvanicum	1600	1444[a]	0[a]	0.00
P. persicaria	1600	1503[a]	21[b]	2.08

IV.3.4 Experiment 4. Viability of different sized achenes after excretion

The proportions of achenes in each size category were estimated; this information together with the dimensions of achenes is each size category is given in Table IV.3. The mean values for achene lengths, widths and size categories were compared between species using analyses of variance and the Student-Newman-Keuls test. Detailed results of these analyses are given in Appendix IV.4. These analyses revealed that the achene lengths and widths differed between size categories within species. The widths but not the lengths were similar ($P = 0.05$) between corresponding size categories for P. lapathifolium and P. persicaria indicating that the achenes of these two species differed in general shape.

The numbers of achenes eaten did not differ between species or size category ($P > 0.05$) with the exception of the low value for the large achenes of P. lapathifolium. This information is shown in Table IV.4; details of the analysis are given in Appendix IV.5. No achenes of P. pensylvanicum remained viable after excretion; however, some viable achenes were retrieved for all size categories of P. lapathifolium and P. persicaria. The percentage values were too small to allow direct comparison by information analysis (Sokal and Rohlf 1969; pg. 565); however, comparisons were made between the actual numbers of viable achenes excreted. Table IV.4 shows that in P. lapathifolium and P. persicaria, viability

Table IV.3 Information concerning the separation of achenes of each species into three size categories. Values in the same column and associated with the same letter are not significantly different at the 5% level. (*) means of 50 randomly chosen achenes per achene size category.

Species and achene size categories	Mesh sizes of sieves used in separation mm.	Achene dimensions* length mm.	Achene dimensions* width mm.	Naturally occurring proportions of achenes in each size category % by weight	Naturally occurring proportions of achenes in each size category % by number
P. lapathifolium					
small	1.19	1.73^{a}	1.43^{a}	7.1	12.4
medium	1.19, 1.41	1.96^{b}	1.70^{b}	74.5	72.9
large	1.41	2.07^{c}	1.87^{c}	18.4	14.7
P. pensylvanicum					
small	2.00	2.77^{f}	2.58^{d}	15.9	21.5
medium	2.00, 2.38	3.07^{g}	2.94^{e}	57.4	58.5
large	2.38	3.29^{h}	3.19^{f}	26.7	20.0
P. persicaria					
small	1.19	2.12^{c}	1.47^{a}	3.6	5.9
medium	1.19, 1.41	2.27^{d}	1.69^{b}	54.1	57.1
large	1.41	2.38^{e}	1.86^{c}	42.3	37.0

Table IV.4 Percentage viability of smartweed achenes of different sizes after excretion by captive cottontails. Each value is the total from three replicates, each of 400 achenes. Values in the same column and followed by the same letter are not significantly different at the 5% level.

Species and achene size categories.	Numbers of viable achenes per cottontail.		% achene viability after excretion
	eaten	excreted	
P. lapathifolium			
small	1092^{ab}	101^{d}	9.26
medium	1117^{ab}	41^{c}	3.70
large	1048^{a}	5^{b}	0.49
P. pensylvanicum			
small	1138^{ab}	0^{a}	0.00
medium	1154^{b}	0^{a}	0.00
large	1041^{b}	0^{a}	0.00
P. persicaria			
small	1115^{ab}	42^{c}	3.77
medium	1171^{b}	34^{c}	2.90
large	1100^{ab}	3^{b}	0.27

after excretion was inversely related to achene size. Achene viability was greater in the smaller fruited P. lapathifolium than in P. persicaria. Details of this analysis are shown in Appendix IV.6.

IV.4 Discussion and conclusions

Field evidence suggested that cottontails (Sylvilagus floridanus) were agents for achene dispersal in at least two species of Polygonum. This field evidence consisted of:

1. direct observations of cottontails feeding from fruiting spikes,
2. many cottontail faeces, containing achenes found near the plants, and
3. the successful germination of achenes of P. lapathifolium and P. persicaria from the faeces (Experiment 1).

Endozoochory can be divided into three stages:

1. attraction of the dispersal agent,
2. transportation by the agent and
3. deposition in a site suitable for growth.

Success (i.e. completion in a viable state) at each stage depends upon chance or effective adaptations possessed by the propagule against hazards encountered. The three stages of endozoochory were investigated by means of experiments and a survey of the literature.

IV.4.1 Stage 1. The achenes as a food source for cottontails

Unless eaten accidentally with other vegetation, the achenes must be attractive as food to the animals. In experiment 1 seeds of Solanum dulcamara were abundant in

cottontail faeces, while plants of this species were scarce at the faeces collection site. This finding suggested an active selection for fruits of this species as food. Such a deduction is not possible for the smartweeds. P. lapathifolium was both abundant at the collection site and its achenes abundant in faeces, P. persicaria was scarce at the collection site and its achenes rare in the faeces. In Britain some selection by partridges for achenes of P. lapathifolium and P. persicaria was noted by Potts (1970).

Potts (1970) has shown that achenes of Polygonum spp., when compared with barley grains, are better sources of nitrogen, magnesium and calcium and only marginally inferior sources of sodium, potassium and phosphorus. Large quantities of starch in the endosperm of ripe achenes provides a good source of food at a time when fat production in cottontails reaches a maximum (Trippensee 1938). The high frequencies with which cottontails, other animals (Ridley 1930) and prehistoric man (Bertsch 1954) have eaten smartweed achenes suggests that bitter flavours which would be detrimental to endozoochory are absent.

Edible diaspores (i.e. dispersal units, van der Pijl 1969) must be recognized as a potential food source by the agent. Animals such as cottontails which are crepuscular or nocturnal feeders (Dalke and Sime 1941) are more dependant upon scent than sight for finding food (van der Pijl 1969). Fruiting spikes contain flowers as well as ripe achenes.

Nectaries are present in these flowers (Knuth 1906) and on the leaf surfaces (Salisbury 1909). Contrasting coloration between the pink perianth segments and blackish achene is perhaps a useful aid for visual recognition of ripe fruits by birds (van der Pijl 1969) and its role as an aid to cottontails cannot be dismissed.

In Middlesex County, cottontails are abundant in riverbank habitats which provide cover and food. Smartweeds growing on open gravel bars usually produce most fruits below 45 cm. Achenes have been eaten from spikes at this height. Laboratory experiments (Expts. 2, 3, 4) showed that cottontails readily eat detached achenes at ground level.

IV.4.2 Stage 2. Transportation of the diaspores by the dispersal agent

Experiment 1 indicated that achenes of P. lapathifolium and P. persicaria could be dispersed by endozoochory. In this experiment the differences in the numbers of each species which germinated under the four germination conditions were not due to these conditions because all viable achenes present had germinated. The large variations probably result from the small sample sizes. Feeding known numbers of achenes to captive cottontails established percentage viabilities. This experiment suggested that achene size was a crucial factor as the species with the largest achenes showed the lowest viability and vice versa. The achenes of P. pensylvanicum and the larger achenes of the other two species were rendered

inviable by mastication, indicating a selection in favour of those species with small achenes. This has also been suggested by de Vlaming and Proctor (1968) for dispersal by water birds. On the other hand, there are probably other selection pressures that operate in favour of large achenes, for example in germination.

Achene viability is determined by the efficiency of mastication and digestion in cottontails and characteristics of the achenes (i.e. shape, size and structure). Van der Pijl (1969) states that mammal dispersed propagules are generally smaller than those that are bird dispersed; because the mammals possess teeth. Achenes of P. pensylvanicum are not dispersed effectively by cottontails but have been eaten and voided in a viable state by migrating ducks. Achenes undamaged by mastication are well protected against digestive juices by their thick ligno-cellulose fruit coats (Woodman 1930). Endosperm and embryo remnants were absent in the faeces indicating that they had been digested from damaged or chipped achenes.

Changes in dormancy due to thinning of the fruit walls (Krefting and Roe 1949; Rick and Bowman 1961) were not observed in the above experiments. Ripe smartweed achenes show natural dormancy (see Chapter V) and if this was broken during endozoochory the seedlings would not survive the winter weather.

The assumption was made that feeding behaviour of cottontails was not altered by captivation. No experiments

were carried out within a month of capture, the animals were provided with a variety of food and water at all times. Feeding behaviour phenomena, such as crepuscular feeding, reingestion of faeces and nocturnal defaecation were not changed by capture; however, a change would probably have occurred in the microorganisms of the intestinal tract (Mr. K. G. McGill, pers. comm.). The regurgitation of large seeds (deVlaming 1967) and caching of food (Tourrette et al. 1971) were not observed in these experiments.

IV.4.3 Stage 3. Deposition of diaspores

The results illustrated in Fig. IV.1 show that most of the ingested achenes are voided shortly after feeding (2-4 hours) for both P. lapathifolium and P. persicaria. A few achenes are retained within the animal for longer durations (to a maximum of between 24 and 48 hours) and thus could be transported further. The time of excretion of whole and fragmented achenes after feeding was similar for P. lapathifolium and P. persicaria. Small differences in the numbers of achenes deposited could have been due to the greater numbers of achenes eaten for P. lapathifolium and the higher viability in this species after excretion. In cases of scarcity, food may be retained in the caecum for long periods of time (Trippensee 1938). Crudén (1966) states that in birds dispersal over long distances is accomplished by external rather than internal transport. De Vlaming and Proctor (1968) give the mean maximum retention times in

Killdeer (Charadrius vociferus L.) for Polygonum bicorne Raf. as 14 hrs. and for Polygonum aviculare L. as 27 hrs which are adequate times for long distance dispersal. Similar data for mallards (Anas platyrhynchos L.) are 1 hr. and 8 hrs. respectively. Proctor et al. (1967) have demonstrated that differences in the structure and function of digestive tracts of water-birds influence both the retention time and ultimate viability of aquatic organisms dispersed in this way. As cottontail movements are relatively restricted compared with migratory birds, dispersal is likely to be relatively local.

The question arises as to whether achenes may be introduced into newly available sites or different habitats by cottontails. In particular, agriculturalists want to know whether potentially weedy species (such as Polygonum spp.) can be introduced into croplands (McAtee 1947). Each of these three species of Polygonum are self-compatible (Mulligan and Findlay 1970) and the successful introduction of one individual to a previously uncolonized site can initiate colonization (Baker 1955).

The trapping of cottontails on the edge of a hardwood forest in southern Ontario by White (1967) indicated that the animals have home ranges of less than ten acres and even within these areas, movement is generally limited. Allen (1939) has shown that cottontail movements are partly predicted by the availability of food. Soybean and corn

fields may be food sources in autumn. It would seem that dispersal of achenes of P. lapathifolium and P. persciaria would only be for short distances, but these distances would be sufficient to enable colonization of frequently re-exposed riverbanks or disturbed soils.

CHAPTER V

ACHENE DORMANCY AND GERMINATION

V.1.1 Introduction

Achenes of smartweeds (P. lapathifolium L., P. pensylvanicum L. and P. persicaria L.) mature in late summer and autumn in southern Ontario. In the riparian habitats where these species are common low temperatures, gravel movements and prolonged flooding during the winter months make immediate germination disadvantageous. Many workers (eg. Ransom 1935; Justice 1941) have shown that most achenes of these species are dormant at maturity. Sells (1965) in Iowa and Porter (1966) in Pennsylvania have shown that achenes of P. pensylvanicum in long term storage exhibit a continuous dormancy which is only absent during the spring of each year. Similar cyclical patterns of dormancy have been found in P. aviculare L. in England (Courtney 1968) and in Amaranthus retroflexus L. (Barton 1945).

Observations by several authors have shown that many smartweed achenes are dispersed into sites unsuitable for germination (eg. deep in the soil or to the beds of water courses) where they remain dormant until re-exposed to favourable conditions (Roberts and Dawkins 1967; Dale 1964; Wesson and Waring 1969). If suitable conditions fail to occur the achenes are capable of remaining viable for extended periods (see Table V.1).

Table V.1 Longevity records for achenes buried in soil.

Species	Duration of viability	Author
P. lapathifolium	6 years	Dorph-Peterson 1924,
P. persicaria		Kjaer 1940
P. pensylvanicum	3.3 years	Justice 1941
P. longisetum	4560 years	Suto 1973*
P. persicaria		
P. hydropiper	50 years (4% viability)	Darlington 1931

* Suto, T., 1973. Personal communication from Prof. Suto of Akita Agricultural Experimental Station, Akita, Japan 010.

While a great deal of information exists concerning dormancy breakage in the laboratory for achenes of several species of Polygonum, there is a lack of studies relating dormancy and germination processes to environmental events in the habitats of the plants. This chapter a) describes experiments which deal with the effects of various environmental factors on dormancy, and b) seeks to identify some of the various environmental "signals" (Amen 1963; Koller 1964) which trigger germination. The effects of dispersal agents on dormancy, germination and viability are described in Chapters III and IV and will not be repeated here.

V.1.2 Source of achenes

Achenes for all experiments described in this chapter were collected from plants of P. lapathifolium, P. pensylvanicum and P. persicaria growing along the banks of the Thames River between Fanshawe Dam, London and the village of Muncey (Latitude 43°01'N, longitude 81°16'W). Details of the climate and other environmental factors of the collection area were given in Chapter I. The collecting procedure was the same as that described in Chapter III. Achenes from the three species were kept separate but no attempt was made to divide them into size or shape categories since this study was concerned primarily with characterizing the dormancy and germination attributes of each species as a whole.

V.2.1 Experiment 1. Preliminary germination tests on fresh achenes

The preliminary investigation consisted of a series of tests in which fresh achenes were put to germinate under a variety of conditions. These were intended to reflect the environmental conditions which might have stimulated or influenced germination on the riverbank immediately after achene fall. The achenes were collected on September 15th (tests 1-18) and October 13th (tests 19-21). Germination tests were initiated on the day of collection. The test conditions and germination results are shown in Table V.2. Tests were continued for 40 days. Each achene was removed from the experiment after germination. Four replicates, each of 100 achenes were used for each species and each test. The achenes were sown in seed flats (tests 1-8) or in glass petri dishes containing two layers of moistened "Greens #450" filter paper (tests 9-21). Achenes were used with perianth segments attached, except in test 15.

V.2.2 Results and discussion (Preliminary experiments)

The majority of mature achenes collected in September showed a dormancy that could not be broken either by a variety of simulated natural conditions or by any of a number of usual laboratory procedures. This dormancy had been lost from at least some achenes in the October collection. The mean daily maximum and minimum temperatures during September, 1968 were 22°C and 12°C, and during October 15°C and 5°C

Table V.2 Preliminary germination tests and their results. Each value is the mean of four replicates, each of 100 achenes.

Test No.	Description	Mean % germination after 40 days		
	Achenes collected Sept. 15th, 1968.	P. lap.	P. pens.	P. pers
1	outdoors, exposed to weather, on riverbank surface	0	0	0
2	as (1) but 1 cm below the surface	0	0	0
3	as (1) but on potting-compost surface	0	0	0
4	as (1) but 1 cm below potting-compost surface	0	0	0
5	in greenhouse, natural day length on surface of riverbank soil, watered daily	1	0	5
6	as (5) but 1 cm below the surface	0.5	0	0
7	as (5) but on surface of potting-compost	0.75	0	2.5
8	as (5) but 1 cm below potting-compost surface	0	0	1.25
9	20°C, light	0.25	0	0
10	20°C, dark except when observations were made	0.25	0	0
11	25°C, light, 14 hrs.; 10°C, dark, 10 hrs.	2.5	0	0
12	30°C, light, 14 hrs.; 15°C, dark, 10 hrs.	2.5	0	0.25
13	35°C, light, 14 hrs.; 20°C, dark, 10 hrs.	3.75	0	1.75
14	25°C, dark, 14 hrs.; 10°C, dark, 10 hrs.	2.25	0	0
15	as (11) but perianth segments removed	0	0	0.25
16	manual abrasion with sandpaper for 1 min., then as (11).	1	2.5	0

Table V.2 (Continued)

Test No.	Description	Mean % germination after 40 days		
	Achenes collected Sept. 15th, 1968.	P. lap.	P. pens.	P. pers
17	submerged for 30 secs: in conc. sulphuric acid, washed, then as (11)	0.75	1.25	0.5
18	suspended 24 hrs. in running tap water, then as (11)	0.25	0	0
	Achenes collected Oct. 13th, 1968.			
19	as (11)	2	0	1.75
20	as (12)	15.5	4	12.25
21	as (13)	100	9.75	40

("Monthly Weather Reports", London Weather Office).

Even though a low percentage of seedlings can germinate in the autumn this percentage would represent substantial numbers of seedlings when the numbers of achenes produced per plant is considered (P. lapathifolium, 19,300; P. pensylvanicum, 3,140; P. persicaria, 1,550; Stevens 1932). Under field conditions the non-dormant achenes of tests 5-21 presumably would have shown an enforced dormancy until the following spring. Autumn germination would only occur during abnormally mild autumns.

Samples of achenes collected in October gave at least some germination, especially when placed under warmer incubator conditions, indicating a gradual shift from "innate" to "enforced" dormancy (see Harper 1957 for terminology) between the September and October collection dates. The germination totals were significantly different for each of the incubator regimes (higher temperatures meant higher germination totals) and between species ($P < 0.01$). The totals for P. lapathifolium exceeded those of the other species. P. pensylvanicum showed the least germination (see Appendix V.1 for details of this analysis).

Achenes which remained ungerminated after 4 weeks were stored in a cold (4°C), moist environment for 6 additional weeks and then placed under the same germinating conditions as described for test 2. Germination exceeded 98% for all tests after this after-ripening treatment.

V.3 Experiments 2-4. Dormancy and viability in achenes stored in natural sites for varying lengths of time

The preliminary germination tests started in September, 1968 demonstrated that fresh achenes were dormant and unlikely to germinate in the year of production. The loss of dormancy in some or all achenes by October, suggested the occurrence of a physiological change within the achenes; this may have been caused by a change in environmental conditions or merely with time or through a combination of the two. Many workers (eg. Justice 1941; Ransom 1935) have found that chilling treatments will break dormancy, hence it is conceivable that cool weather in October may have been responsible for this loss of dormancy. The lack of high temperatures during October would have prevented autumn germination in the field thus resulting in enforced dormancy. In Experiment 2 the effects of the winter environment (prolonged exposure to low temperatures) on dormancy were monitored. In control treatments, achenes were kept in a constant cold moist environment over winter to determine whether such conditions alone were responsible for after-ripening.

Submergence and burial of achenes frequently occurs as a result of floods, soil movements and dispersal. For various lengths of time, achenes come to lie in sites very different from one another in water content, depth of burial etc. Experiment 3 was designed to determine how dormancy and viability could be affected by storage in

sites with different water regimes. In Experiment 4, the effects of burial on achene dormancy and viability were investigated.

V.4 Methods and Materials

V.4.1 Experiment 2. Influences of the winter environment on achene dormancy

Freshly collected achenes were stored over winter under two sets of conditions.

a) Outside on a gravel bar from which the achenes for this experiment had been collected. This bar was inundated periodically between mid October and the end of April of each year.

b) In moist conditions in a cold (4°C) storage chamber with 14 hr. darkness and 10 hr. light daily.

Achenes of the three species were collected on November 8th 1968 in the manner described previously. These achenes had already been exposed to 7 nights on which the temperature had reached 0°C or less. 2800 achenes were stored under condition a) in seven fine mesh nylon bags (30 x 30 cm), securely pegged to the substrate. The mean maximum and minimum temperatures; and the extent of inundation during the storage period are given in Table V.3. The 2800 achenes stored in condition b) were placed in petri dishes containing moistened filter papers. 100 sound achenes were placed in each dish. There were four replicates for each withdrawal date and species.

The achenes were retrieved from storage after 0, 1,

Table V.3 Mean maximum and minimum daily temperatures and the extent of inundation during Experiment 2.

	Mean Max. daily temp. C.	Mean Min. daily temp. C.	Extend of flooding
November 1968	44.1	30.8	Intermittent inundation
December 1968	30.4	16.0	Intermittent inundation
January 1969	27.6	14.9	3 weeks continuous inundation
February 1969	28.9	13.5	3 weeks continuous inundation
March 1969	36.2	20.5	continuously inundated
April 1969	55.9	33.9	continuously inundated

2, 4, 5, 9 and 15 weeks and put to germinate at 25°C, light, 14 hr.; 10°C dark, 10 hr. for 40 days. For this test the achenes were placed in fresh petri dishes containing moistened (15 ml of distilled water) filter papers with 100 achenes per dish. All dishes were examined daily for germination and germinated achenes removed. Four replicates for each storage site, duration and species were used. After 40 days all ungerminated achenes were after-ripened at 4°C for a further 6 weeks. After this additional treatment the germination test was repeated as a test for viability.

V.4.2 Experiment 3. Effects of moisture on achene dormancy

Achenes of all three species were stored outdoors under 5 moisture regimes to determine the influence of the storage site on subsequent germination. Detailed descriptions of the sites are given on the page preceding Fig. V.3. The sites were:

a) bed of a rapidly flowing portion of the Thames River
b) bed of a pond near site (a)
c) surface of a gravel bar adjacent to site (a)
d) 60 cm beneath the surface of a gravel bar, near site (c)
e) dry in 250 ml plastic flasks on the surface of a gravel bar, near site (c).

To recognize the separate effects of temperature, moisture and aeration on germination, additional sets of achenes were stored under the following artificial conditions,

f) dry, in a seed room

g) submerged in sealed plastic flasks partly filled with Thames River water and stored in the seed room

h) submerged and under the same conditions as (g) but in flasks filled with Thames River water

i) submerged and under the same conditions as (h) but flasks filled with freshly boiled distilled water

j-m) in cold storage (4°C) otherwise similar to storage treatments (f)-(i)

Achenes used in this experiment were gathered on October 2nd 1970 and had experienced no temperatures below 4°C. They were placed in the above mentioned storage treatments on the same day. Four replicates, each of 100 achenes, were provided for each treatment. Each sample was put into a fine mesh nylon bag which was firmly secured (conditions a-d) or put into a 250 ml plastic flask (conditions e-m). Samples were removed from storage on February 10th, March 28th, May 15th and August 30th 1971. After retrieval the achenes were counted and classified as;

i) sound but dormant. These were tested for germinability as in Experiment 2 and were then classified as dormant or non-dormant.

ii) germinated in storage.

or iii) non-viable (i.e. rotted during storage).

Descriptions of weather before and during the period of storage and of the Thames River water during the time of

storage were given in Chapter I.

V.4.3 Experiment 4. Effects of burial on achene viability, dormancy and germination

The effects of burial at three depths were examined for achenes of the three species by measuring subsequent germination at a soil surface influenced by fluctuating water levels.

Achenes of the three species were collected on September 30th 1969 just after a cold spell when the temperature approached the freezing point. On this day, samples of 100 sound achenes each were placed into nylon bags (30 x 30 cm containing soil). These were buried at three depths in clay-loam soil at the Experimental Field Station, University of Western Ontario (see Fig. V.1) as follows:

a) 60 cm below the surface (i.e. beneath the normal ploughing depth)

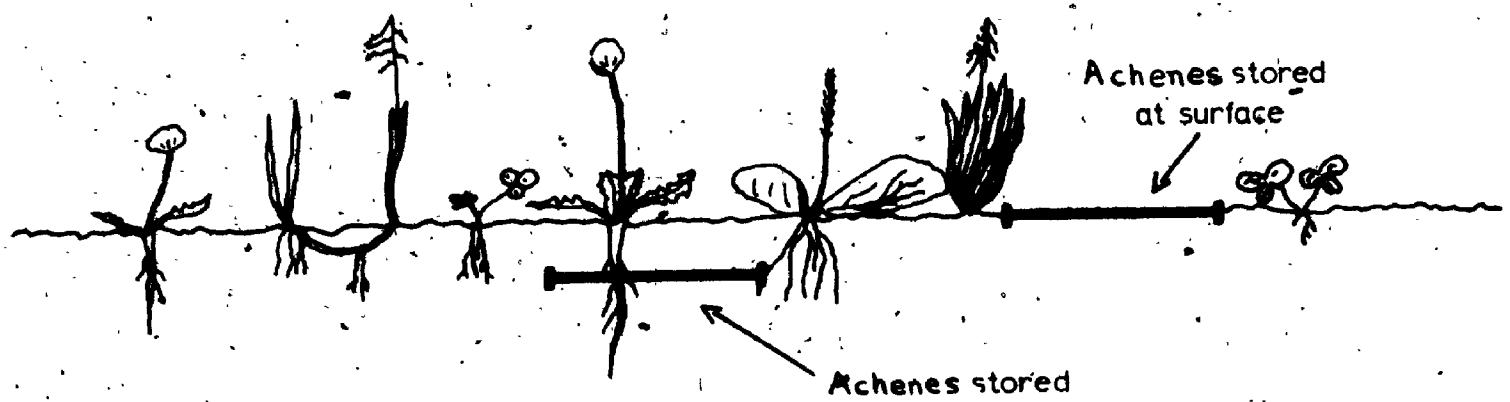
b) 6 cm below the surface (i.e. within the normal ploughing depth)

c) at the soil surface

The site used for this storage experiment had been under pasture for many years but had been ploughed a year before the experiment was conducted. On April 10th, June 20th and August 20th 1970, nylon bags representing all treatments were retrieved.

On the day of retrieval the achenes were sown 1 cm

FIG. V.1 SITES OF ACHENE BURIAL.



Achenes stored 60 cm deep

Species abundant on storage site include.

Poa compressa
P. pratensis
Taraxacum officinale
Plantago major
P. rugelii
Trifolium spp.

SOIL DESCRIPTION

Position	Texture	Approx. length of time frozen	pH	P	K	Ca	N ($dS\ NO_3^-$)
Surface	Clay-loam	2 Months	7.8 - 8.0	V. high	Low - v. high	V. high	V. low - low
6 cm deep	Clay-loam	1 Month	7.6 - 8.0	High - v. high	Low - v. high	V. high	V. low - medium
60 cm deep	Clay	Not frozen	7.6 - 8.0	V. low - low	Low - medium	V. high	V. low - low

beneath the surface of a sterilized clay-loam soil in seed flats. In order to simulate conditions in a moist habitat, the flats were placed in a polythene-lined trough containing 2 cm of water; this level was allowed to increase with rainfall (see Plate 7). Bird-scaring devices were positioned around the trough to discourage achene removal. The flats were examined bi-weekly for seedlings, which were counted and carefully removed. The bags containing stored achenes and the flats were arranged in a random design.

Daily temperatures and rainfall were obtained for the germination period (1970 and 1971) from the London Weather Office located five miles from the Experimental Field Station.

V.5 Results

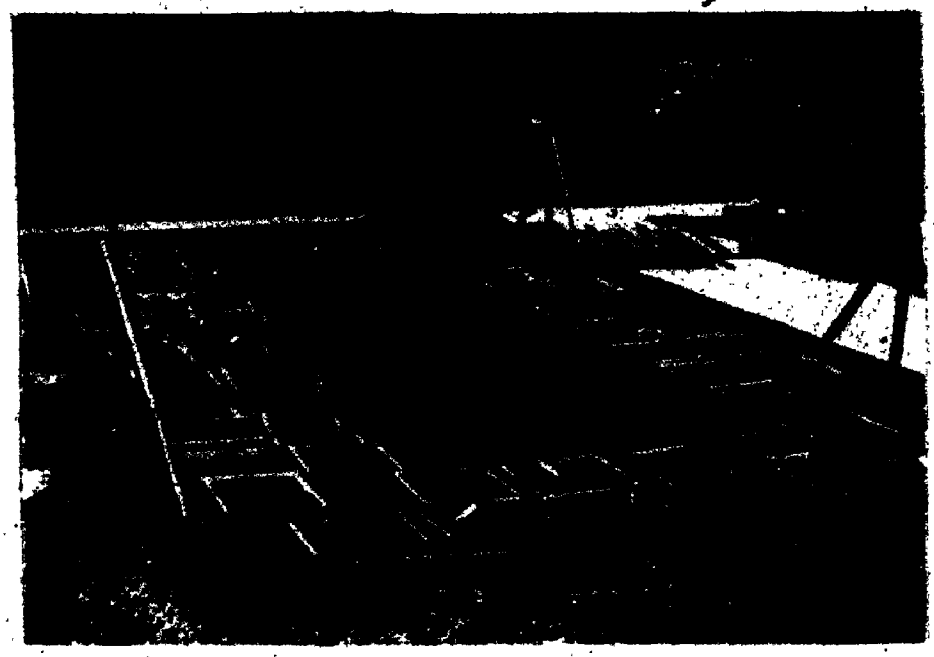
V.5.1 Experiment 2

Achenes stored outdoors during the winter months or stored in artificially cold, moist conditions showed highly significant losses of dormancy ($P < 0.001$) between successive retrieval dates. For each of the three species, virtually complete germination was recorded after 15 weeks cold storage. The germination period was prolonged after short periods of cold storage, whereas after longer periods it was "quasi-simultaneous" (Salisbury 1970). No germination occurred after the first 30 days of any germination test.

Highly significant differences ($P < 0.01$) in germination totals existed between species, except at the final retrieval date (i.e. after 15 weeks of storage) when virtually all seeds

PLATE 7

Photograph of water trough used in Experiment 4, Chapter V to measure germination of achenes in fluctuating soil moisture conditions.



of all species germinated. Comparisons of total percentage germinations are shown in Figure V.2. The highest germination totals were recorded for P. lapathifolium and the lowest for P. persicaria for all retrieval dates (except the final one). More than 90% germination was recorded from achenes of P. lapathifolium which had experienced artificial cold storage for one week.

With the exception of achenes from the final retrieval date, storage under natural and artificial cold conditions had significantly different effects ($P < 0.01$) on subsequent germination. Achenes stored outside were more dormant than those stored at a constant 4°C.

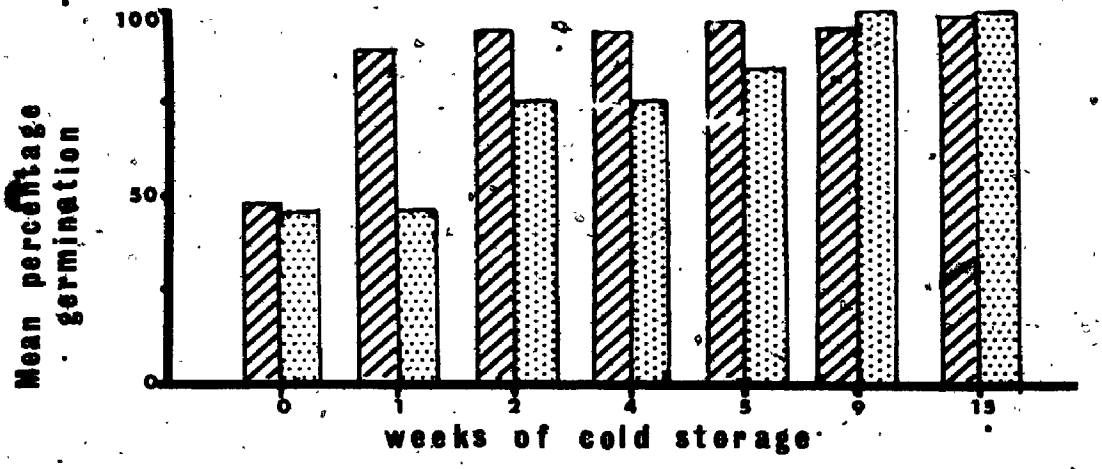
The germination data were compared using information analysis (see Appendix III.1). Detailed results of the analyses are shown in Appendix V.2.

V.5.2 Experiment 3

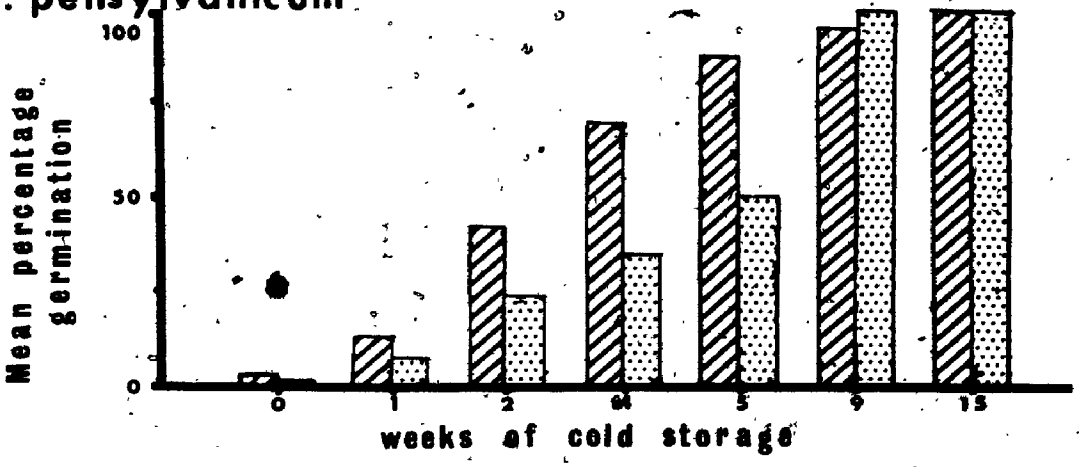
Two types of data are presented from this experiment. Fig. V.3 shows the total germination percentages for samples of achenes retrieved on four dates in one year, from 13 storage sites. These are achenes which remained dormant while in the storage site but germinated readily in the laboratory upon retrieval. Fig. V.4 shows the condition of achenes after one year's storage. These achenes are classified as; dormant (achenes which germinated readily in the laboratory plus those which required chilling before germination took place), non-viable, and germinated in the storage site (before

FIG. V.2 GERMINATION OF ACHENES AFTER COLD STORAGE IN EACH OF TWO SITES FOR VARIOUS TIME PERIODS. (Diagonally stripped histograms represent achenes stored at constant 4°C; stippled histograms those stored outside over winter).

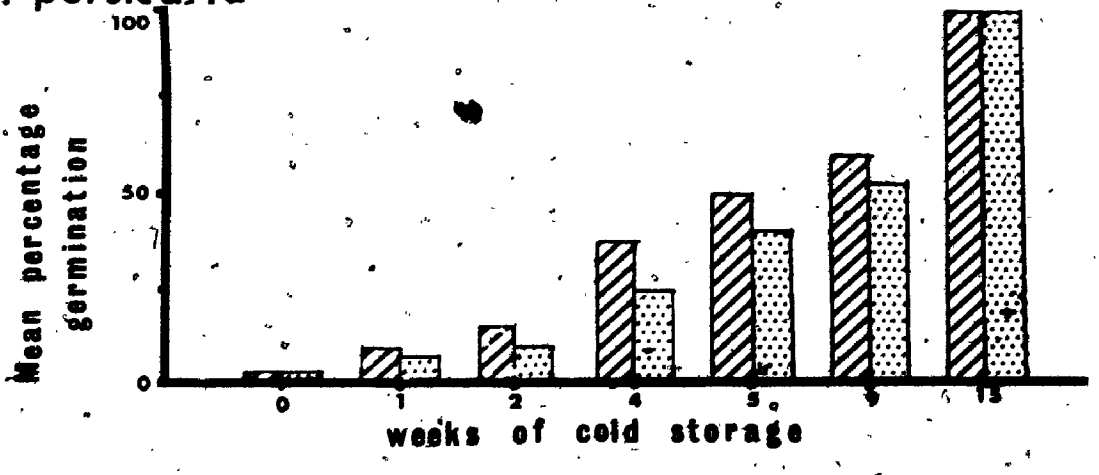
a) P. lapathifolium



b) P. pensylvanicum



c) P. persicaria



Key to site symbols used in Figures V.3 and V.4.

a) Submerged by at least 60 cm of water on the bed of a rapidly flowing section of the Thames River in the vicinity of the University of Western Ontario.

b) Submerged by at least 60 cm of water on the bed of a pond near site (a). This pond was stagnant during most of the year but occasionally inundated by river water during winter floods.

c) On a gravel bar surface adjacent to site (a). This site was periodically flooded between mid October and the end of April each year.

d) In nylon bags, 60 cm beneath the surface of a gravel bar, near site (c). Otherwise similar conditions to (c).

e) In plastic bottles, dry on the surface of a gravel bar near site (c). Otherwise similar conditions to (c).

f) Dry at a constant temperature of 22±2°C under weak natural daylight and in an atmosphere of less than 40% relative humidity.

g) Submerged in nylon bags in 100 ml of Thames River water within sealed 250 ml plastic flasks and stored in the seed room described in (f).

h) Submerged and under the same conditions as (g) but in 250 ml flasks filled with Thames River water.

i) Submerged and under the same conditions as (h) but

j-m) In cold storage (4°C) otherwise similar to storage treatments (f) to (i).

FIG. V.3 TOTAL PERCENTAGE GERMINATION OF ACHENES AFTER STORAGE IN 13 SITES FROM OCTOBER 1970 UNTIL RETRIEVAL IN FEBRUARY (1), MARCH (2), MAY (3) AND AUGUST (4). (See "Methods and Materials", Experiment 3 for descriptions of storage sites (a-m); (o) signifies no germination).

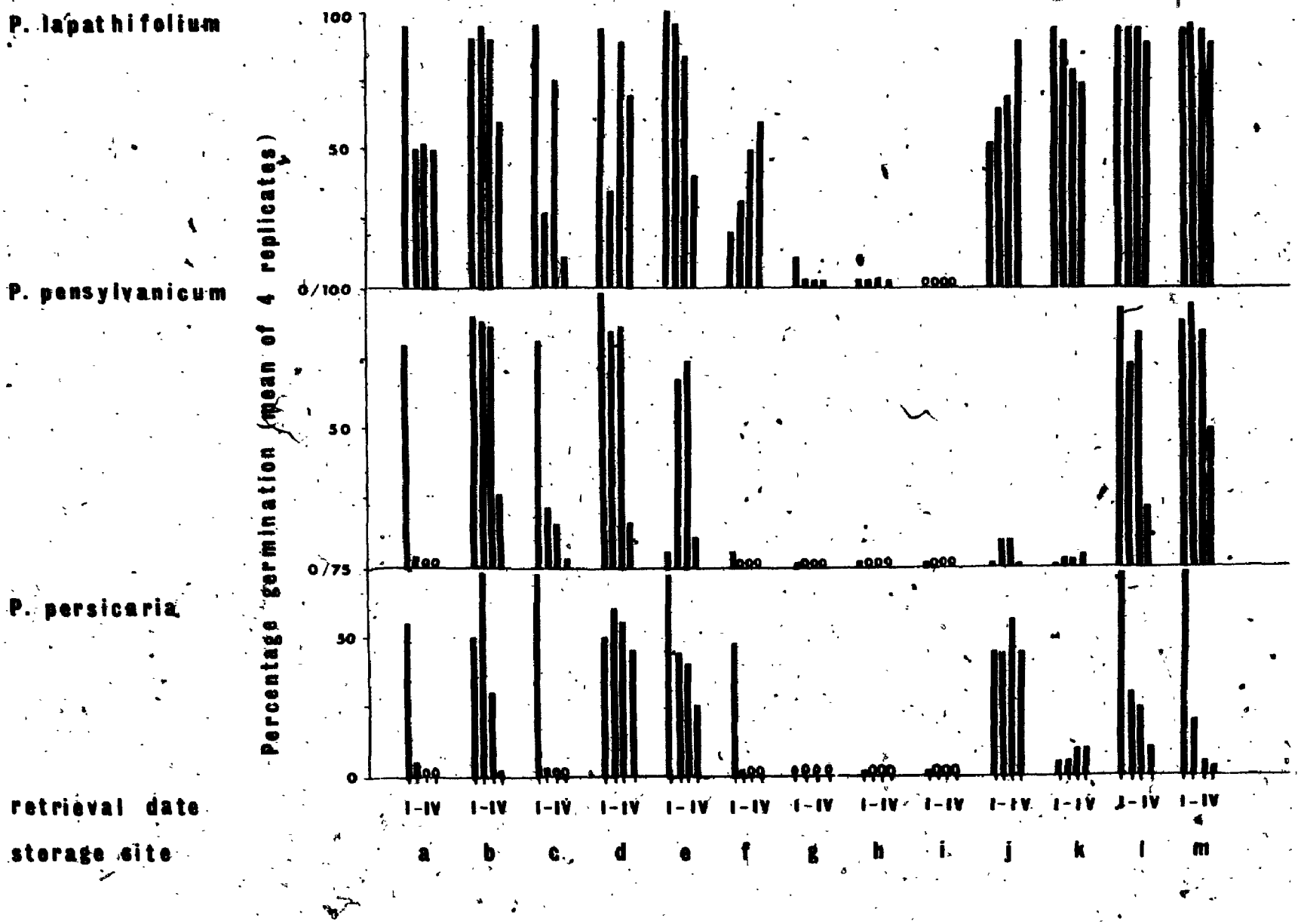

P. lapathifolium
P. pensylvanicum
P. persicaria
Percentage germination (mean of 4 replicates)
100
50
0/100
50
0/75
50
0
I-IV
retrieval date
storage site
a b c d e f g h i j k l m

FIG. V.4 PERCENTAGES OF ACHENES WHICH GERMINATED IN SITU, SHOWED DORMANCY OR NON-VIABILITY AFTER 11 MONTHS STORAGE UNDER VARIOUS CONDITIONS.

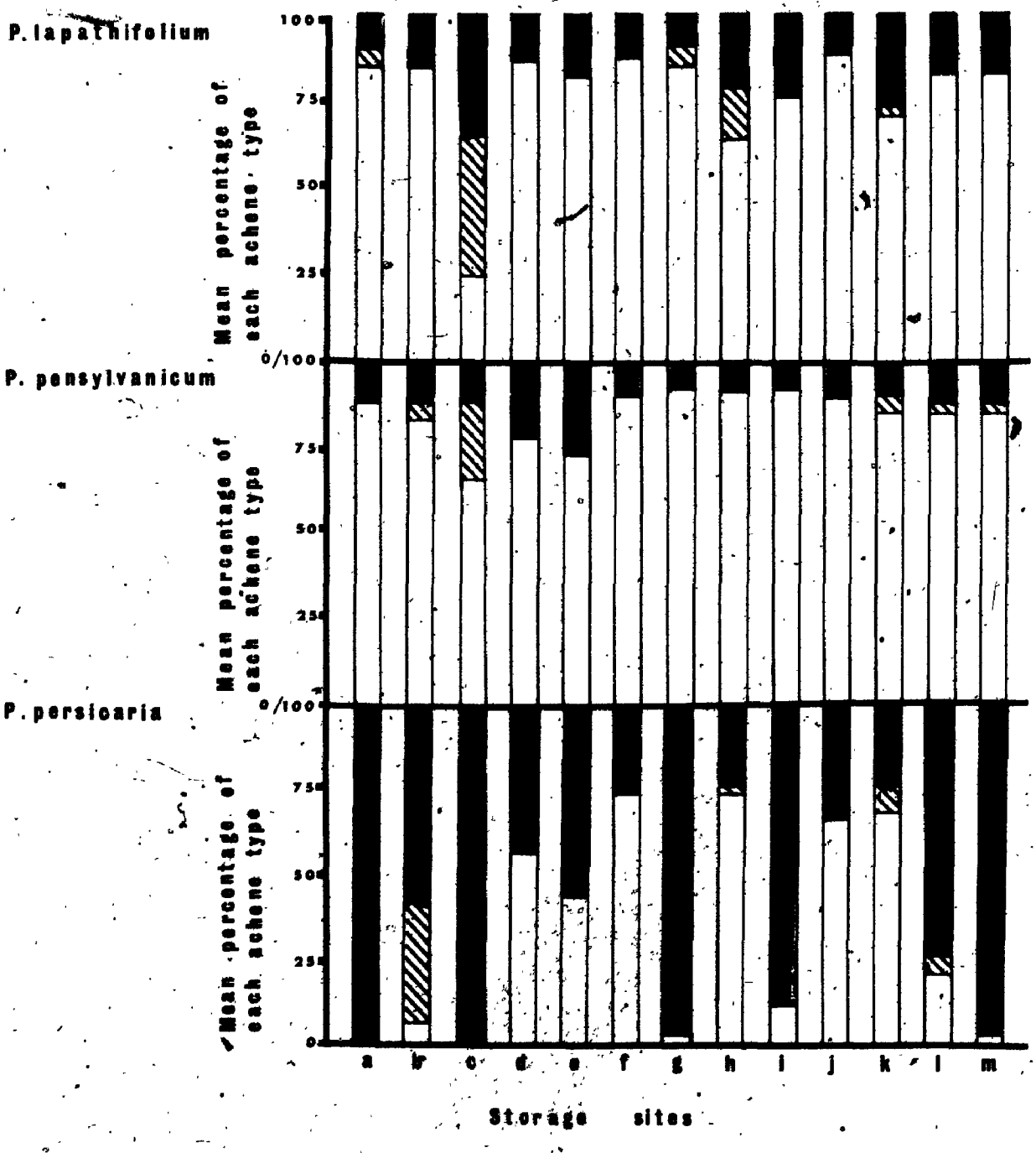
% non-viable achenes after storage for eleven months

% achenes germinated in situ

% achenes viable but dormant

The y-axis shows the percentages of achenes of each condition; these values are means of 4 replicates of 100 seeds each.

See Key to site symbols on the page preceding Fig. V.3.


P. lapathifolium
P. pensylvanicum
P. persicaria
Mean percentage of each achene type
100
75
50
25
0/100
0
a
b
c
d
e
f
g
h
i
j
k
l
m
Storage sites

retrieval). The two figures must be considered together for a complete understanding of the effects of storage on achene dormancy and germination. Total germination scores were compared using information analysis (see Appendix V.3 for details of the results).

Cyclical dormancy - Patterns of increasing dormancy from early retrieval dates to those later in the year were not as obvious as those found by previous workers (Sells 1965; Porter 1966). Such trends were not apparent for P. lapathifolium, were present for some treatments using P. pensylvanicum and if present in P. persicaria, were masked by high non-viability.

Dry storage - Dry storage at room temperature (f) resulted in moderate (P. lapathifolium) ~~or~~ low subsequent germination totals (especially P. pensylvanicum). Dry storage outdoors (e), where the temperature varied greatly, showed higher subsequent germination scores, as did storage at a constant 4°C (j) for P. lapathifolium and P. persicaria. Achenes of P. pensylvanicum remained dormant after constant low temperature dry storage, thus differing from those stored dry under variable temperatures (e). No dry achenes of any species germinated during storage and after one year these achenes showed high viability when compared with those of other treatments.

Wet storage - Germination after cold wet storage was high, whether river water (l) or tap water (m) was used, however, the presence of air (k) caused subsequent germination

totals to be very low for P. pensylvanicum and P. persicaria but not for P. lapathifolium. In the field the influence of aeration on wet storage was again important. Achenes of P. pensylvanicum and P. persicaria stored in running water (a) showed low germination totals when compared with those from, presumably, less aerated pond water (b). This effect was again not noticeable for P. lapathifolium. Achenes showed virtually complete dormancy after wet storage at room temperature (g, h, i). Germination in storage occurred in storage occurred in achenes stored on the gravel bar surface, at room temperature under moist conditions (P. lapathifolium), in flowing river water (P. persicaria) and in cold wet storage (P. pensylvanicum). Under wet conditions achenes of P. persicaria were very susceptical to rotting ~~(Fig. V.4)~~.

~~Temperature - Although~~ influenced by the presence of water and aeration, the general effects of temperature can be summarized as follows. Most achenes stored at room temperature were dormant after retrieval and required chilling before germination took place. Those achenes subjected to outdoor temperatures showed moderate to complete germination totals (especially P. lapathifolium). Those of P. lapathifolium stored under constant cold conditions showed almost 100% germination, whereas those of the other species would only germinate in moist storage in the absence of air under this temperature regime.

V.5.3 Experiment 4

Achenes which had been stored at three depths in agricultural soil and then retrieved and sown on three dates during the subsequent year showed well defined germination flushes. These commenced during late April, late June and late August 1970, regardless of the previous storage depth, species or sowing date. In some treatments a fourth and final flush occurred in April 1971. Mean germination data for each flush are given in Fig. V.5. Fig. V.6 shows that the flushes followed periods of high rainfall during the year.

Surface stored achenes were not available for the June and August sowing dates as most had germinated in situ before retrieval.

Information analysis was used to compare final germination scores and to compare flush sizes for each treatment. In most cases there were no significant differences ($P > 0.05$) in final germination totals between species, sowing times or soil storage depths (see Appendix V.4). Most variation was caused by the relatively high value for P. lapathifolium (mean for all treatments, 87.3%) and the relatively low value for the August sowing date (mean for all treatments, 74.4%). No significant difference ($P > 0.05$) in germination response existed between the achene burial depths (6 cm and 60 cm).

FIG. V.5 GERMINATION FLUSHES FROM ACHENES PREVIOUSLY BURIED AT 3 DEPTHS AND RETRIEVED ON 3 DATES.

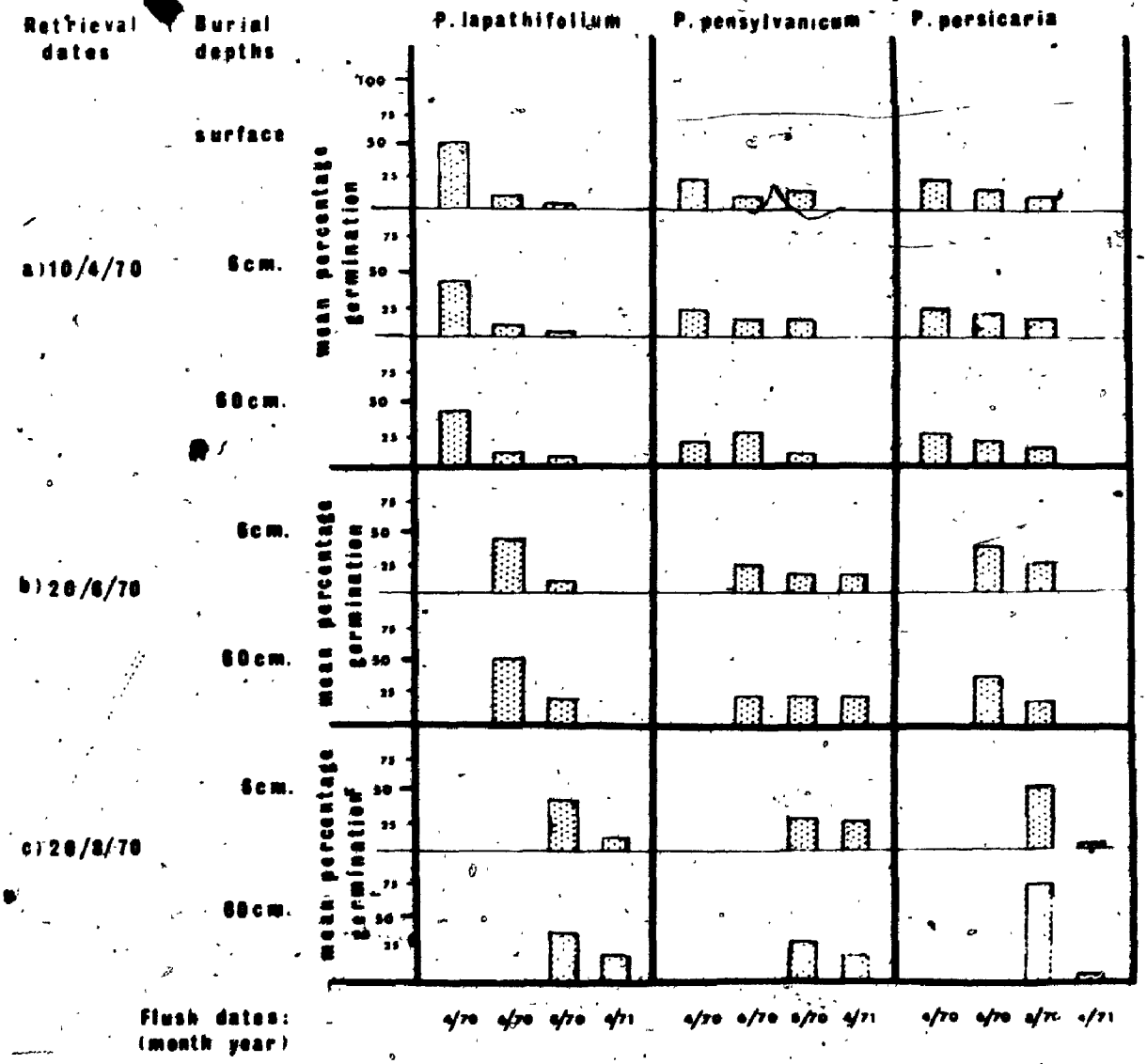
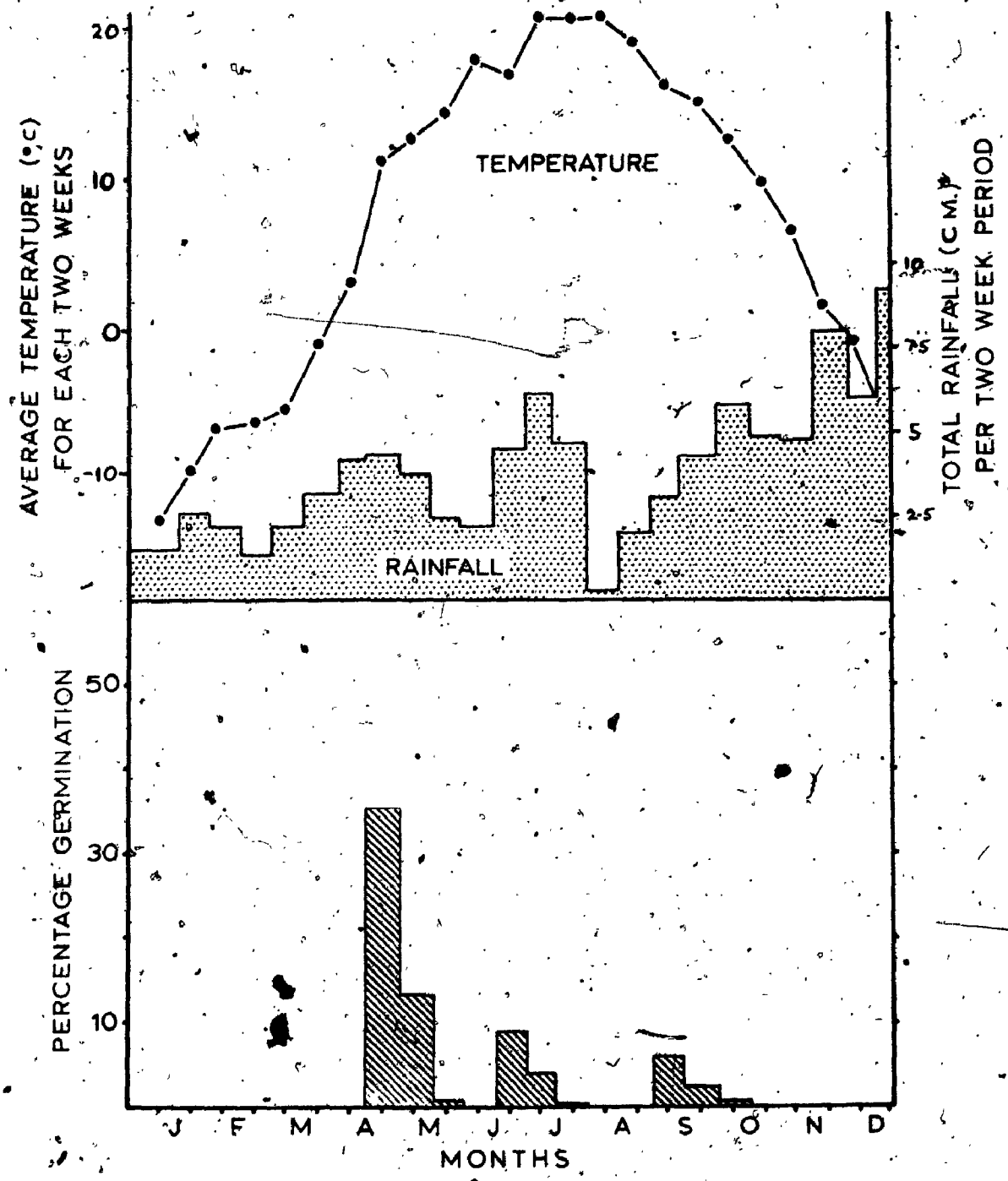

Retrieval dates
Burial depths
P. lapathifolium
P. pensylvanicum
P. persicaria
surface
a) 10/4/70
8cm.
60cm.
b) 28/6/70
8cm.
60cm.
c) 28/8/70
8cm.
60cm.
mean percentage germination
100
75
50
25
Flush dates: (month year)
4/70 6/70 8/70 4/71

FIG. V.6 CORRELATIONS BETWEEN GERMINATION PATTERN, PRECIPITATION AND TEMPERATURE.


AVERAGE TEMPERATURE (°C)
FOR EACH TWO WEEKS
20
10
0
-10
TEMPERATURE
RAINFALL
TOTAL RAINFALL (C.M.)
PER TWO WEEK PERIOD
10
7.5
5
2.5
PERCENTAGE GERMINATION
50
30
10
J F M A M J J A S O N D
MONTHS

The number of flushes was determined by the sowing date. Achenes sown in April showed flushes in April, June and August; those sown in June showed flushes in June and August and in some treatments the following April, those sown in August showed flushes in August and the following April. In all cases the successive flushes decreased significantly ($P < 0.01$) in size (Figures V.5 and V.6).

The first germination flush occurred in April, June or August depending on the date of sowing. A 3-factorial analysis (see Appendix V.4) showed that the first flushes were of significantly different sizes, with P. lapathifolium showing the highest germination (mean for all treatments, 67.6%) and P. pensylvanicum the lowest (mean for all treatments, 32.4%). Germination following the August sowing (mean for all treatments, 56.4%) was significantly greater than that following the April sowing date (45.1%); however, storage depth had no significant influence on the size of the first flush. Similar analyses of the second and third flushes showed significant differences in most species comparisons and sowing date comparisons. For both flushes, P. lapathifolium showed the lowest germination and P. pensylvanicum the highest and in both cases the autumn sowings showed the lowest germination.

V.6 General discussion

Achenes of P. lapathifolium, P. pensylvanicum and P. persicaria exhibit innate, enforced and induced dormancies. Each type of dormancy is adaptive for survival during specific

environmental conditions in the riverbank habitat. Propagules in which the embryos are not mature or are mature but unable to germinate because of some property within the propagule at the time of dispersal are said to exhibit innate dormancy. Those which are capable of germination but fail to germinate because of environmental limiting factors show enforced dormancy. Induced dormancy occurs when propagules which at one time are fully capable of germination acquire a dormancy which may be caused (and released) by various environmental or internal stimuli (Harper 1957).

Ripe achenes of the three species collected from riverbanks in Southern Ontario were almost 100% dormant at the time of collection in September. This innate dormancy ensured that autumn germination, which would have been fatal on flooded riverbanks in freezing temperatures, did not take place. These results agreed with those of Ransom (1935), Justice (1941), Timson (1965b), Porter (1966) and Hammerton (1967a) who have found little or no germination in fresh achenes of P. lapathifolium and/or P. pensylvanicum. No amelioration of the strong dormancy in fresh achenes was found in tests using a variety of light, temperature and substrate conditions. Similarly, no increases in germination resulted from scarification and leaching pre-treatments on fresh seeds. Ransom (1935) and Justice (1941) had similar results for their scarification and leaching treatments. Timson (1965b) and Hammerton (1967a, 1967b) have found that achenes from different collections differed in the degree

of fresh achene dormancy, a few strains showed no dormancy at all.

Some achenes collected in October had lost this innate dormancy; however, these achenes would only germinate at room temperatures and no germination was witnessed in the field. Further experiments with these samples showed a gradual loss of innate dormancy in the field or more dramatically at a constant 4°C in moistened conditions. It was noted that longer after-ripening periods would result in more complete and more rapid germination, when warm temperatures were provided. Apparently, cold temperatures in the field broke innate dormancy but maintained an enforced dormancy until warmer temperatures in the spring, when germination was possible.

Many authors recommend after-ripening at constant low 0-6°C temperatures in moist or wet conditions for breaking dormancy in Polygonum species (Dorph-Peterson 1924, Ransom 1935, Justice 1941, Yamada 1954, Bayer and Bucholtz 1957, Bayer 1958, Maquire and Overland 1959, Timson 1965b, Porter 1966, Hammerton 1967a, 1967b). Moisture is apparently essential for after-ripening according to Justice (1941); however, results of germination tests on dry stored achenes in experiment 3 differed from his results for P. lapathifolium and P. persicaria. The conditions and period of after-ripening required for breaking innate dormancy varied for achenes of different plants and populations (Ransom 1935, Justice 1941,

Hammerton 1967a, 1967b) and also between years for the same population (Justice 1941). Such differences account for discrepancies in after-ripening times and conditions suggested by various authors.

The period of after-ripening may be shortened by previous dry storage (Ransom 1935, Justice 1941, Porter 1966), acid scarification (Ransom 1935, Hammerton 1967b, Porter 1966), mechanical scarification (Bayer 1958, Hammerton 1967b) or pericarp removal (Ransom 1935, Bayer 1958). The possibility that gravel movement may cause seed coat abrasion which facilitates germination in riverbank plants has been explored by Lubke and Cavers (1969).

Few achenes germinate when buried or submerged but do so relatively readily if brought to the surface or brought into laboratory germinating conditions. This type of enforced dormancy prevents uneffective germination of those achenes falling to the beds of streams between rock particles on gravel bars or buried by sedimentation. The results of experiments 3 and 4 showed that buried achenes of P. lapathifolium and P. pensylvanicum retained viability whilst those of P. persicaria lost some or considerable viability in such conditions. Great losses of viability occurred at the gravel bar surface where conditions are most suitable for germination but most susceptible to extreme fluctuations of temperature and water content (Taylorson 1970, Stoller and Wax 1974). Enforced dormancy was especially

evident where achenes were stored in the absence of air (i.e. in stagnant pond water or in sealed containers of boiled water), those in aerated water (i.e. in flowing streams or aerated flasks of water) rapidly assumed induced dormancy or became inviable.

Retrieval from burial at any time of the year resulted in flushes of germination which commenced after periods of high rainfall. Initial flushes were significantly larger than subsequent ones; however, the germination flushes in P. pensylvanicum were relatively even sized compared with those of P. lapathifolium which showed a very large initial flush and low subsequent ones. The theories of Sells (1965) and Porter (1966) that certain Polygonum species show cyclical patterns of germinability are not strongly supported by the results described here for Ontario plants. Only for a few treatments using P. pensylvanicum did achenes removed from burial or submergence in the spring give larger germination totals than those recovered later in the year. Justice (1941) and Ransom (1935) found that air drying especially if rapid caused a hard induced dormancy in P. lapathifolium and P. pensylvanicum and less so in P. persicaria.

Results of the preceding experiments have shown that the achenes of P. lapathifolium and P. pensylvanicum are well adapted to survival on the riverbank, showing high viability percentages after storage in many wet sites. Germination strategies between the two species differ. Most achenes of

P. lapathifolium germinate during the first period of favourable conditions, whereas, those of P. pensylvanicum show more intermittant germination, a larger number of achenes remaining dormant until the next spring. Both show germination flushes whenever the soil is moist and the temperature mild. Achenes of P. persicaria show low viability when stored in wet sites; however, higher viabilities and intermittant germination in agricultural soils contribute to the weediness of this species. In riverbank soils P. persicaria has a relatively small "seed bank" (for concept of "seed banks" see White and Harper 1970) which has to be replenished annually; whereas, those of the other species are more resistant to deterioration.

CHAPTER VI

SEEDLING ESTABLISHMENT

VI.1 Introduction

Sedimentation and erosion along water courses during periods of fluctuating water levels result in the formation of physically and chemically heterogeneous soils (lithosols) deposit as bars. They are common soil type along the North Branch of the Thames River in southern Ontario. In this region, they are composed primarily of limestone particles of various sizes. They are porous and dry when exposed; however, daily and seasonal fluctuations in the river level cause rapid changes in the level of the water table and nutrient status within a bar.

Although new soil surfaces are frequently exposed or laid down, plant colonization is limited to species and individuals tolerant of fluctuating water tables, burial and erosion. The number of seeds that germinate and become established is related to the number of "safe-sites" offering conditions that fit the requirements of seeds and seedlings (Harper, Clatworthy, McNaughton and Sagar 1961). The diversity of seedlings is determined by the diversity of the safe-sites (Harper, Williams and Sagar 1965) and the resulting vegetation is a blend of species normally considered as weeds, marsh or woodland plants, forming a distinct flora, and having the common ability to survive in such a habitat.

The smartweeds; Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L. occur frequently in such habitats along the North Branch of the Thames River and were the subjects of the following experiments. Each of these species inhabits a different kind of microhabitat on gravel bars (see Chapter II). P. lapathifolium grows largest in the low wet areas adjacent to the river; whereas, P. pensylvanicum produces more biomass in the higher, drier areas away from the river. P. persicaria is relatively infrequent but occurs in many parts of the gravel bank. These microhabitats are characterized by differences in matrix structure, porosity, distance from the waters edge and presumably differences in erosion and deposition. It was unknown whether the differences in spatial distribution of the species reflected differing dispersal patterns, germination requirements, establishment requirements or combinations of these factors. Chapter V described the germination requirements and germination patterns of each species. It is the purpose of this chapter to describe two experiments in which seedlings of each species were grown under a variety of simulated riverbank conditions and in which establishment, productivity and aspects of growth between species were compared. The factors under consideration include:

i) the depth of the water table,

ii) the soil type,

iii) the depth of burial of germinated achenes.

VI.2 Methods and Materials

The achenes used in both experiments had been collected from plants growing on gravel banks along the North Branch of the Thames River within the City of London, Ontario. After collection they were stored in a moist, cold (4°C) environment until required for experimentation in May of the following year. In May they were germinated under a daily regime of 25°C for 14 hr. in the light and 10°C for 10 hr. in darkness.

Germinated achenes (radicles 5 mm long) were used in both experiments. Twenty four achenes were used for each treatment in Experiment 1 and twenty for each treatment in Experiment 2. During experimentation the seedlings were grown in an unheated greenhouse (21° ± 6°C) under natural daylight. Emergence of seedlings was taken as the appearance of the cotyledons above ground level. Additional germinated achenes were used to replace any which failed to emerge in Experiment 1. In Experiment 2, replacement seedlings were used to maintain a total of 15 plants per treatment. If more than 15 plants remained in any treatment, the excess seedlings were randomly designated and removed. Treatments in both experiments with eight or less emerged seedlings were not included in later statistical analyses of harvest data.

Forty two days after germination, the plants were harvested by carefully washing the soil from the roots. At harvest, any flowering was noted. If flower buds or open flowers, visible to the naked eye, were present at the shoot

apex this meant that a plant was flowering. Stems and roots were separated, dried in an oven (60°C) for ten days and weighed.

VI.2.1 Experiment 1. Effects of water level on emergence, productivity and flowering

Fifteen seed boxes were placed in a water trough (87 x 154 x 15 cm) which was maintained full of rain water. Each seed box (25 x 25 x 7 cm) containing soil was raised or lowered so that its soil surface was in one of the following positions relative to the water level in the trough;

a) submerged, 4.5 cm below the water level. This treatment was abandoned after three weeks as no seedlings emerged. Another treatment (4.5 cm above the water level, no additional watering) was substituted for it.

b) at water level. No surface watering.

c) 10 cm above the water level. No surface watering.

d) 18 cm above the water level. No surface watering.

e) Freely drained, not connected to the water table. This treatment was surface watered daily with rain water at the rate of 0.25 $cm/cm^2/day$.

In treatments c) and d) several bottomless seed boxes were stacked in order to achieve the required heights. The soils and water were allowed to stand for two weeks before achenes were sown.

The soil was a mixture of riverbank sand and potting compost (1:1 by volume). Descriptions of the chemical and

physical qualities of the two soil components are given in Table VI.1. Riverbank lithosolic soil was not used as its heterogeneous nature would have added further unknown variables to the experiment. The effects of soil texture on seedling establishment are examined in Experiment 2. Germinated achenes were sown 1 cm beneath the soil surface.

The treatments were arranged in the following way. The 15 seed boxes were placed in a 5 x 3 pattern. Three boxes for each of the five treatments were arranged randomly in the trough and in each there were three rows of eight seedlings, each row being of a different species and again arranged in a random order. For any one treatment there were twenty four seedlings per species.

Seedling emergence was recorded. The plants were harvested six weeks after the planting date and the following characters measured; total dry weight of individual plants, root dry weight/total dry weight per plant, length of shoot, length of root and occurrence of flowering.

VI.2.2 Experiment 2. Effects of soil type and depth of burial on seedling emergence and plant productivity

The physical, hydrological and chemical qualities of riverbank soils along the Thames River, vary considerably. In some places water currents have sorted particle sizes into fairly homogeneous deposits but in most places they are very mixed (lithosols). The nutrient status depends on many factors; nutrients of the watershed soils, amount of variation,

Table VI.1 Physical and chemical properties of the soils used in Experiments 1 and 2. (The largest values for the components of each soil type are indicated by *)

Dry weight analysis Particle size and water content as % of fresh wet weight.	Potting compost	clay	sand	gravel	lithosol
Particle size:-					
<35 mm.	4.60	1.70	0.05	4.60	43.80*
2.00-35 mm.	5.20	0.50	0.50	73.70*	8.00
0.21-0.50 mm.	34.40*	14.80	92.10*	21.34	23.30
0.11-0.21 mm.	7.90	16.30*	0.40	0.00	4.40
0.05-0.11 mm.	4.70	9.80	0.10	0.04	1.40
<0.05 mm.	23.80	25.80*	0.10	0.20	7.10
Water	19.40	31.10*	6.75	0.12	12.00

Table VI.1 (Continued)

Chemical analysis	Potting compost	clay	sand	gravel	lithosol
pH	7.0	8.0	8.0	8.0	8.0
P	V.high	V.high	High-V.high	low-medium	Low
K	High-v.high	V.high	High-V.high	V.high	low-medium
Ca^{++}	V.high	V.high	High	High	V.high
NO_3^-	V.high	Low	V.low-low	V.low	medium
NH_4^+	High	medium	medium	Low	medium

leaching and the nature of the bedrock. Run-off from agricultural or urban land may add further nutrients and pesticide residues. The following five soil types were used in this experiment, they were taken from riverbank deposits of simulated a very rich agricultural soil (as in 1). Their qualities were examined at the time of collection. For each soil type a sample was thoroughly mixed and tested by means of a particle size analysis and with a Helige-Truog Soil Combination Kit. The results are presented in Table VI.1.

1. Potting compost; a mixture of clay-loam, Sphagnum peat and fertilizer.
2. Clay-silt from a bar in Medway Creek (a tributary stream of the Thames), London.
3. Sand, from a riverbank deposit, North Branch, Thames River, London.
4. Gravel, from a riverbank deposit, North Branch, Thames River, London.
5. Lithosol, heterogeneous riverbank deposit, North Branch, Thames River, London.

Seedlings of riparian species are subjected to fluctuating soil-water levels (examined in Experiment 1) and also to the associated effects of sedimentation and erosion. The latter effects were examined in this experiment for each of the soil types described above, by sowing germinated achenes at four depths in the soil;

a) on the surface

b) 1.0 cm beneath the surface

c) 2.0 cm beneath the surface

d) 7.5 cm beneath the surface

The experimental design was as follows. Each of the twenty soil type - burial depth combinations (treatments) was prepared in a single seed box (32 x 50 x 7 cm). The twenty seed boxes were arranged in a random design on a seedling establishment bench and each contained three rows of twenty seedlings each. Each row was of a different species of Polygonum. The seed boxes were watered daily at the rate of 0.25 $cm/cm^2/day$. The experiment was set up and watered for a week before the achenes were sown.

The parameters measured were; the total seedling emergence three weeks after planting and total dry weight of individual plants, six weeks after planting.

VI.2.3 Analysis of data

Two kinds of data were collected from the two experiments described in this chapter.

i) Data as frequencies.

The ultimate numbers of seedlings to emerge and the numbers of plants to flower after six weeks of growth were recorded for the various treatments. To find any association between species and soil conditions these frequency data were analysed by means of R x C tests of independence using the information statistic. Such a test is accurate if the sample size is large (eg. >200 Sokal and Rohlf 1969) and the

minimum expected frequency is not less than 2 or so (Snedecor and Cochran 1967). Data recorded in these experiments rarely fell below either of these values, thus making the use of correction terms or data pooling unnecessary in most cases. Comparisons between pairs of soil conditions and between pairs of species were examined using STP analysis (Sokal and Rohlf 1969).

ii) Data involving continuous variables

The dry weight and measurement data from both experiments were subjected to Bartlett's tests of homogeneity of variances (Sokal and Rohlf 1969). The raw data were found to be heteroscedastic in all cases (see Appendix VI.2). These results suggested that competition had exaggerated differences between small and large individuals by the time of harvest. Logarithmic and square root transformations were then applied and Bartlett's test repeated on each. Favourable results to Bartlett's test after transforming the data was found in one test of Experiment 1 (root length data which had been logarithmically transformed). A two way analysis of variance was used on these data followed by the Student-Newman-Keuls test for multiple comparisons among means. Where analysis of variance was inappropriate in Experiment 1, multiple comparisons were made by STP, a method based on U, the Wilcoxon-Mann-Whitney statistic (Sokal and Rohlf 1969). In Experiment 2 multiple comparisons were made using an approximate test of equality of means (Sokal and Rohlf 1969).

VI.3.1 Results

VI.3.2 Experiment 1

VI.3.2a Emergence of seedlings from soils with water tables at different levels relative to the soil surface

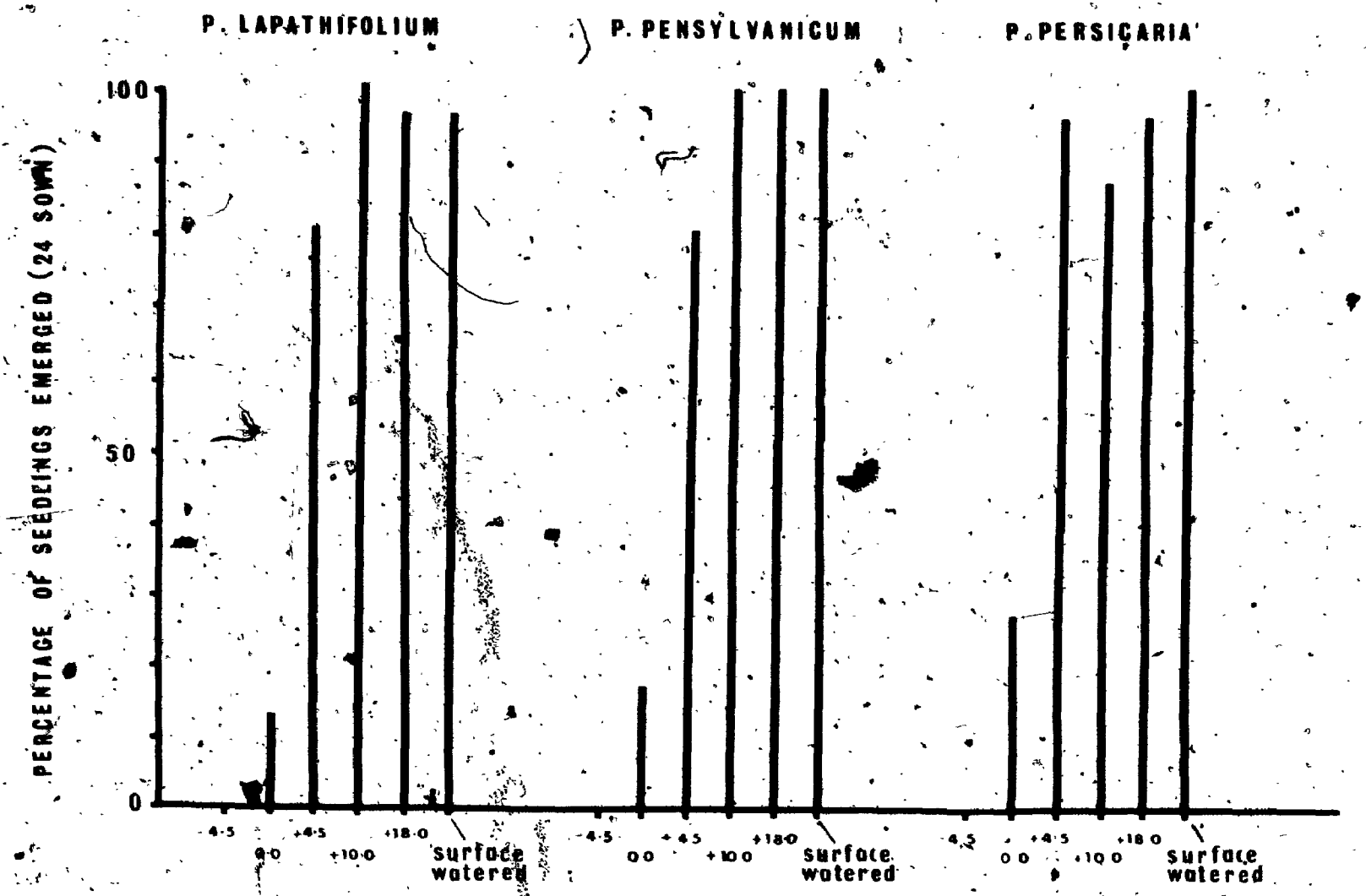
The findings are presented in the bar diagram, Figure VI.1. Differences between species are not significant ($P > 0.05$) for any one of the soil water conditions, see Appendix VI.1. Seedlings previously sown in submerged soil did not emerge and those on a soil surface level with the water table showed poor emergence (12 - 25%). The remaining four soil-water conditions (4.5, 10.0, 18.0 cm above water level and surface watered only) gave significantly higher seedling emergence of at least 78% ($P < 0.05$); however, these four values did not differ between each other. A summary of analyses is presented in Appendix VI.1 and 2.

Treatments showing poor seedling emergence (i.e. submerged and waterlogged soils) were drained and abandoned three weeks after the planting date. As the soils dried, most of the seedlings emerged. An inhibition of seedling growth under high soil-water content is suggested by these observations; however, it is important to note that seedlings can remain viable for several weeks under these conditions.

VI.3.2b Total dry weight and shoot length of plants grown under four soil-water regimes

The dry weight and shoot length data are presented as means, standard errors and ranges in Figures VI.2 and

FIG. VI.1 FINAL EMERGENCE OF PREGERMINATED ACHENES AT THE SOIL SURFACE AFTER PLANTING ONE CENTIMETRE DEEP IN SIX SOIL WATER REGIMES.


P. LAPATHIFOLIUM
P. PENSYLVANICUM
P. PERSICARIA
100
50
0
PERCENTAGE OF SEEDLINGS EMERGED (24 SOWN)
-4·5
0·0
+4·5
+10·0
+18·0
surface watered
POSITION OF SOIL SURFACE RELATIVE TO WATER LEVEL (CM.)

VI.3. The two characters are considered together as they showed similar trends.

Wide ranges were especially noticeable in treatments where the mean values were high. Wide ranges of values within treatments suggested that severe competition had occurred by the time of harvesting, resulting in exaggerated differences between large and small individuals.

The lowest mean dry weights and shoot lengths occurred in the wettest soil-water treatment (4.5 cm above water level) but were also low where the soil was watered from above only. In the latter treatment, P. pensylvanicum was the tallest species but its height was not significantly different from that of P. lapathifolium ($P > 0.05$). Both species were significantly taller than P. persicaria. Maximum dry weights and shoot lengths were found for individuals planted at 10.0 and 18.0 cm above the water level. Plants of P. pensylvanicum and P. persicaria were heavier at 18.0 cm above the water level while those of P. lapathifolium were heaviest and tallest at 10.0 cm above the water level. However, the latter were not significantly taller but heavier ($P > 0.05$) than plants in the 18.0 cm treatment. See Appendix VI.3 and 4 for a summary of analysis results.

VI.3.2c Root weight as a percentage of total dry weight

A comparison of the results presented in Table VI.2 and those of dry weights in Figure VI.2 shows that the root as a percentage of total dry weight was greater for small

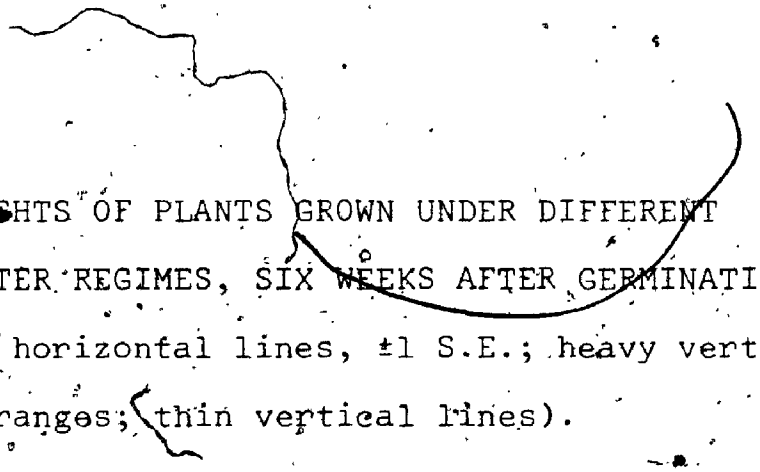


FIG. VI.2 DRY WEIGHTS OF PLANTS GROWN UNDER DIFFERENT SOIL WATER REGIMES, SIX WEEKS AFTER GERMINATION. (Means; horizontal lines, ±1 S.E.; heavy vertical lines, ranges; thin vertical lines).

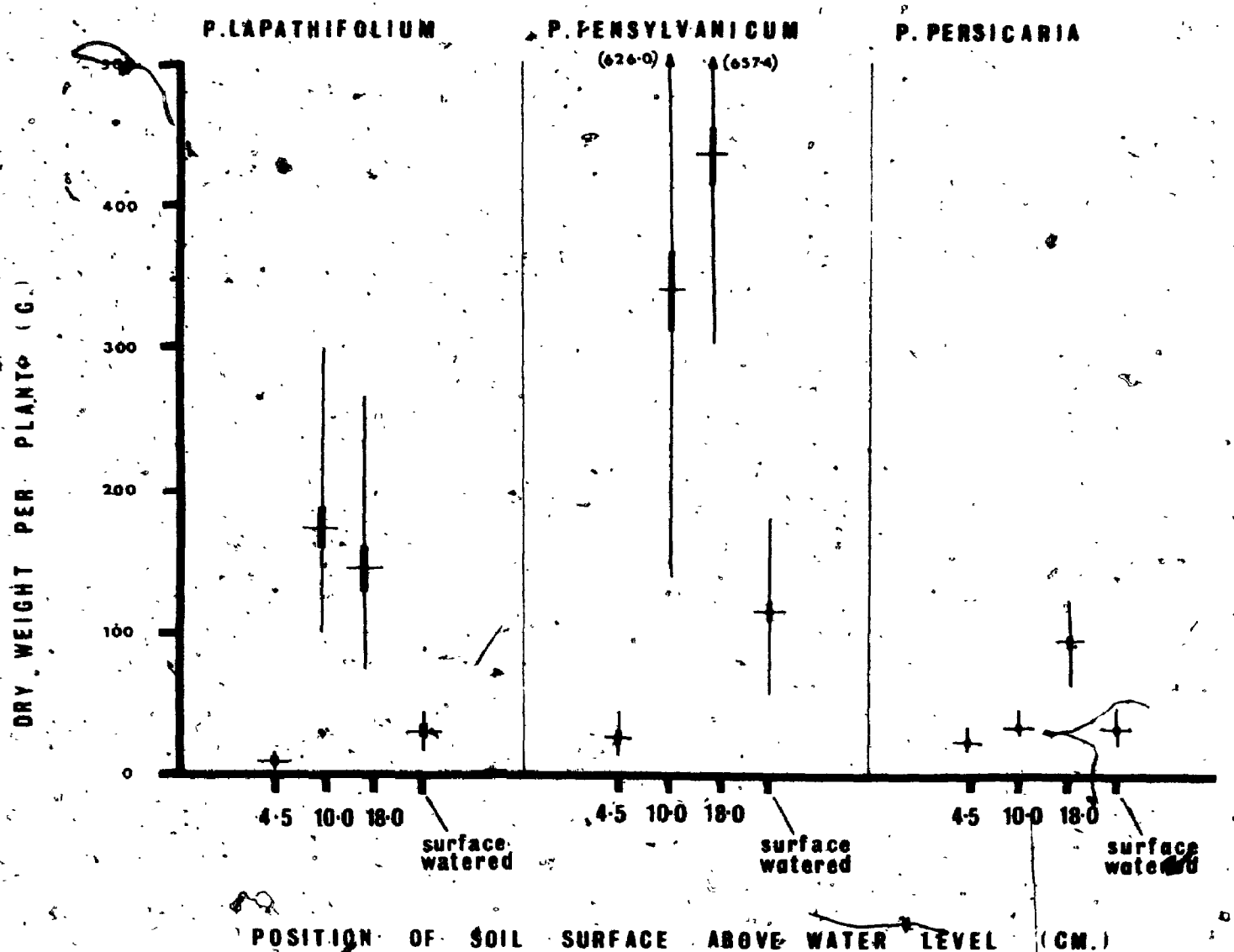

P. LAPATHIFOLIUM
P. PENSYLVANICUM
P. PERSICARIA
(626·0)
(657·4)
DRY WEIGHT PER PLANT (G.)
400
300
200
100
0
4·5
10·0
18·0
surface watered
4·5
10·0
18·0
surface watered
4·5
10·0
18·0
surface watered
POSITION OF SOIL SURFACE ABOVE WATER LEVEL (CM.)

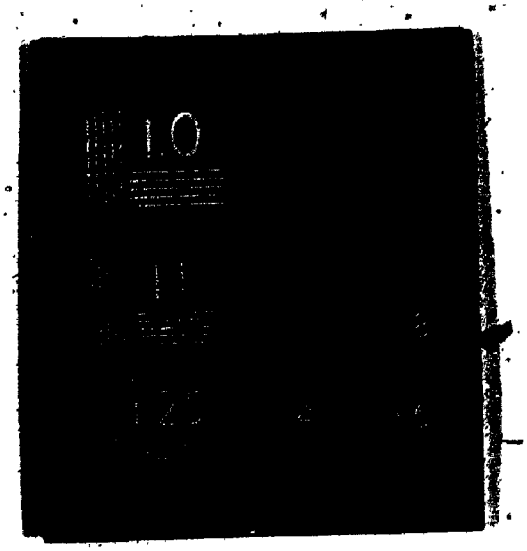
FIG. VI.3 SHOOT LENGTHS OF PLANTS GROWN UNDER DIFFERENT SOIL WATER REGIMES, SIX WEEKS AFTER GERMINATION. (Means; horizontal lines, ±1 S.E.; thick lines, ranges; thin lines).

Table VI.3 Percentages of plants flowering after six weeks growth under six different soil water regimes (24 plants/treatment). Values associate with the same letter were not significantly different ($P > 0.05$). Low values not associated with a letter were too small to be used in comparisons.

Soil water regime	*P. lapathifolium*	*P. pensylvanicum*	*P. persicaria*
soil surface 4.5 cm above water	0	0	0
soil surface 10.0 cm above water	79[a]	79[ab]	75[a]
soil surface 18.0 cm above water	4	96[b]	17[d]
soil, watered from above only	46[ac]	79[ab]	33[cd]

4 5

OF/DE



species flowered in the wettest soil where substantial numbers of plants had survived (4.5 cm above the water level). Most plants of P. pensylvanicum (at least 79%) flowered under the remaining soil-water conditions. For P. lapathifolium and P. persicaria, the flowering percentage was low or moderate on the drier soils (18.0 cm above the water level or surface watered) but highest at 10.0 cm above the water table.

VI.3.3 Experiment 2

VI.3.3a Emergence of seedlings planted at different soil depths in different soil types

Results of information analysis (Appendix VI.8) revealed several general trends (see Table VI.4). The highest values were obtained for seedlings planted on the surface or at 1 cm deep (these were not significantly different from each other, $P > 0.05$) and decreased with planting depth. At the 7.5 cm planting depth, seedling emergence was very poor (usually 0) with the exception of P. persicaria in sandy and clay soils and also P. pensylvanicum in clay soils, all of which showed high emergence. Of the soil types, higher emergence occurred on potting compost, clay and sand than on either lithosols or gravel.

Pairwise comparisons between species and between treatments showed some differences. P. lapathifolium appeared to be more sensitive to planting depth than other species, with no emergence at the 7.5 cm depth and emergence was variable from 2.0 cm depending on soil type. P. pensylvanicum

Table VI.2 Root dry weight as a percentage of total dry weight for six week old plants grown under six soil water regimes. (±1 standard error quoted for each mean, ranges given in brackets)

Soil water regime	P. lapathifolium	P. pensylvanicum	P. persicaria
soil surface 4.5 cm above water	45.8 ± 2.1 (34,70)	34.0 ± 2.7 (19,59)	37.8 ± 3.2 (24.54)
soil surface 10.0 cm above water	12.6 ± 0.4 (10,17)	12.4 ± 0.4 (8,17)	52.6 ± 4.5 (43.68)
soil surface 18.0 cm above water	9.8 ± 0.4 (7,12)	12.0 ± 0.6 (9,23)	12.1 ± 0.3 (9,14)
soil watered from above only	16.4 ± 1.0 (5,26)	16.9 ± 1.0 (9,30)	8.2 ± 0.9 (1,21)

plants (i.e. 4.5 cm above water level, all species) than it was for large plants regardless of species. Plants of P. lapathifolium and P. pensylvanicum watered from the surface only had a larger root dry weight/total dry weight percentage than P. persicaria, the latter value was significantly lower than that for any other species or treatment ($P < 0.05$). A summary of analysis results is given in Appendix VI.5.

VI.3.2d Root length

Analyses of variance of root length (Appendix VI.6) showed a significant interaction between the species and soil-water condition terms. The most variability occurred between soil-water conditions ($P < 0.001$); however, variability between species was also significant ($P < 0.05$). Figure VI.4 shows that plants growing in the wettest soil (4.5 cm above water level) had the shortest roots; however, the plants were also smaller in total size in this treatment. P. persicaria exhibited long roots relative to the size of the plants. The roots of plants grown in the drier soils (10 cm and 18 cm above water level) were the longest; however, those from the surface watered treatment were long considering the plant size. A summary of analysis results is given in Appendix VI.6.

VI.3.2e Flowering of plants grown under different soil-water conditions

These data are presented in Table VI.3 and the analysis results are summarized in Appendix VI.7. No plants of any

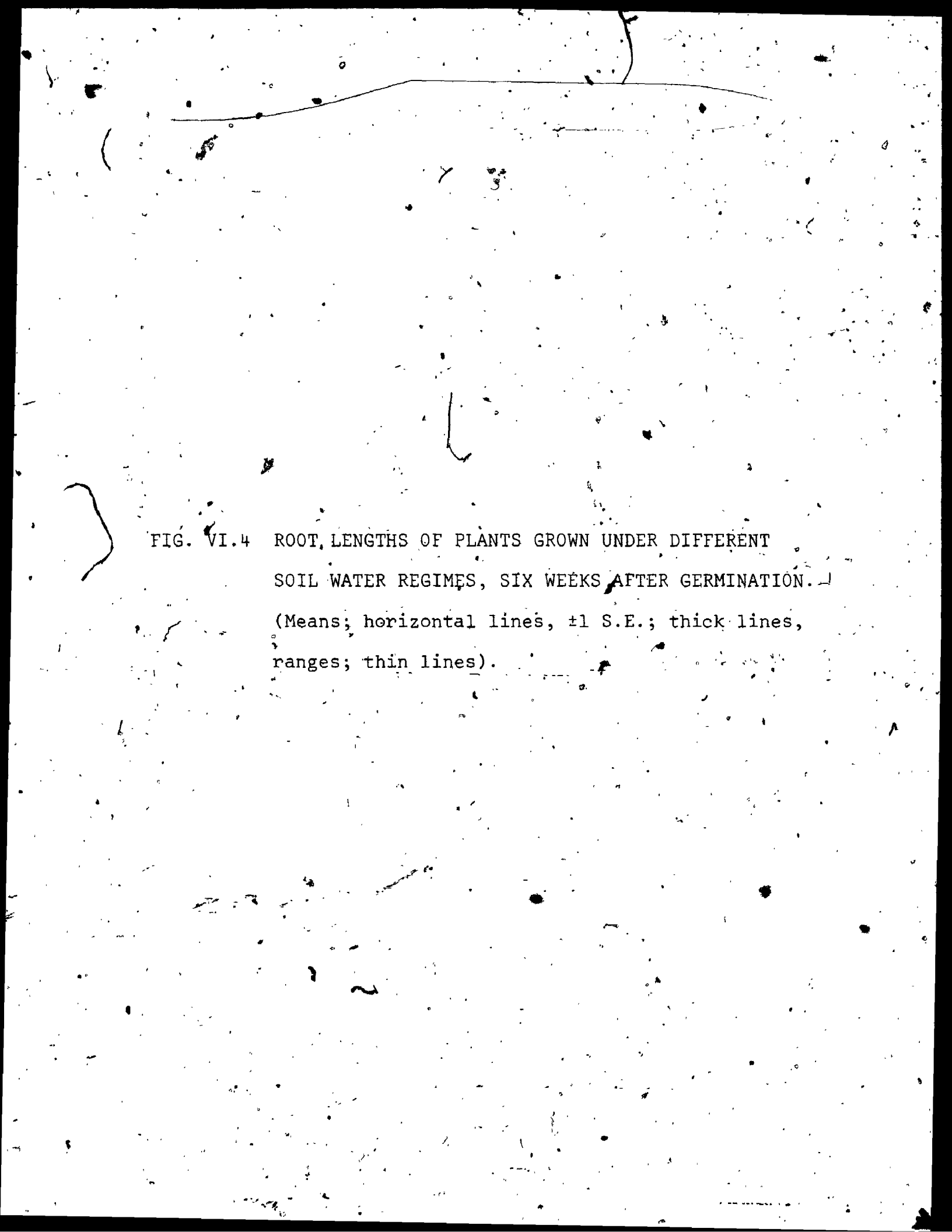


FIG. VI.4 ROOT LENGTHS OF PLANTS GROWN UNDER DIFFERENT SOIL WATER REGIMES, SIX WEEKS AFTER GERMINATION. (Means; horizontal lines, ±1 S.E.; thick lines, ranges; thin lines).

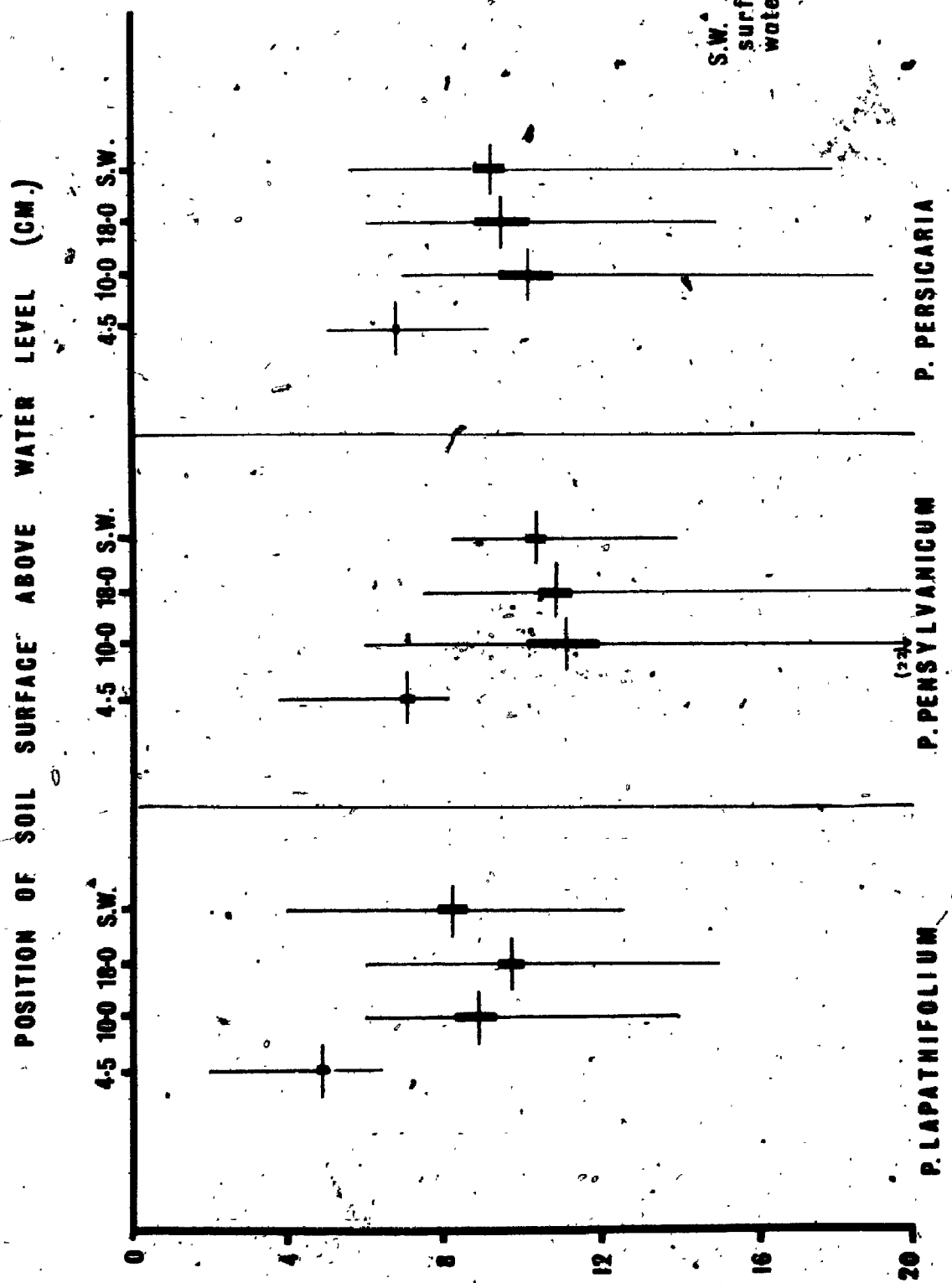

S.W. = surface watered
P. PERSICARIA
P. PENSYLVANICUM
P. LAPATHIFOLIUM
4-5 10-0 18-0 S.W.
POSITION OF SOIL SURFACE ABOVE WATER LEVEL (CM.)
0
4
8
12
16
20
MEAN ROOT-LENGTH PER PLANT (CM.)

Table VI.3 Percentages of plants flowering after six weeks growth under six different soil water regimes (24 plants/treatment). Values associate with the same letter were not significantly different ($P > 0.05$). Low values not associated with a letter were too small to be used in comparisons.

Soil water regime	P. lapathifolium	P. pensylvanicum	P. persicaria
soil surface 4.5 cm above water	0	0	0
soil surface 10.0 cm above water	79[a]	79[ab]	75[a]
soil surface 18.0 cm above water	4	96[b]	17[d]
soil, watered from above only	46[ac]	79[ab]	33[cd]

species flowered in the wettest soil where substantial numbers of plants had survived (4.5 cm above the water level). Most plants of P. pensylvanicum (at least 79%) flowered under the remaining soil-water conditions. For P. lapathifolium and P. persicaria, the flowering percentage was low or moderate on the drier soils (18.0 cm above the water level or surface watered) but highest at 10.0 cm above the water table.

VI.3.3 Experiment 2

VI.3.3a Emergence of seedlings planted at different soil depths in different soil types

Results of information analysis (Appendix VI.8) revealed several general trends (see Table VI.4). The highest values were obtained for seedlings planted on the surface or at 1 cm deep (these were not significantly different from each other, $P > 0.05$) and decreased with planting depth. At the 7.5 cm planting depth, seedling emergence was very poor (usually 0) with the exception of P. persicaria in sandy and clay soils and also P. pensylvanicum in clay soils, all of which showed high emergence. Of the soil types, higher emergence occurred on potting compost, clay and sand than on either lithosols or gravel.

Pairwise comparisons between species and between treatments showed some differences. P. lapathifolium appeared to be more sensitive to planting depth than other species, with no emergence at the 7.5 cm depth and emergence was variable from 2.0 cm depending on soil type. P. pensylvanicum

Table VI.4 Percentage emergence of pregerminated achenes (20 sown per treatment) three weeks after sowing at various depths in several soil types. Values associated with the same letter were not significantly different ($P > 0.05$). Low values not associated with a letter were too small to be used in comparisons.

Soil type	Sowing depth	P. lap.	P. pens.	P. pers.
Potting compost	0.0 cm	95de	95de	100^{e}
	1.0 cm	100^{e}	50^{cde}	95de
	2.0 cm	45^{bcd}	95de	80de
	7.5 cm	0	0	0
Clay	0.0 cm	85de	90de	95de
	1.0 cm	100^{e}	80de	80de
	2.0 cm	100^{e}	95de	95de
	7.5 cm	0	65^{cde}	55^{cde}
Sand	0.0 cm	100^{e}	85de	100^{e}
	1.0 cm	95de	100^{e}	100^{e}
	2.0 cm	50^{cde}	95de	65de
	7.5 cm	0	25^{abc}	90de
Gravel	0.0 cm	85de	100^{e}	100^{e}
	1.0 cm	10^{a}	65^{cde}	10^{a}
	2.0 cm	0	80de	15^{ab}
	7.5 cm	0	0	0
Lithosols	0.0 cm	95de	60^{cde}	0
	1.0 cm	100^{e}	85de	95de
	2.0 cm	10^{a}	85de	70de
	7.5 cm	0	0	0

and P. persicaria seedlings were capable of emergence from 2.0 cm and in some soils (clay and sand) from 7.5 cm. All seedlings of P. persicaria planted on the surface of gravel showed good establishment but on lithosols all failed to emerge; however, examination of those planted at the 1 cm depth showed the opposite trend.

VI.3.3b Dry weights of plants in the five soil types

Mean values for dry weight, their standard errors and ranges (logarithmic scale) are illustrated in Figure VI.5 and in Appendix VI.9. Plant size within each species varied considerably according to soil type. For example, the mean dry weight for plants of P. pensylvanicum grown in potting compost (planting depth 2.0 cm) was 382.9 g; whereas, those grown in sand (surface planted) weighed only 5.4 g. In general, growth in potting compost and clay exceeded that of other soil types, with plants grown in sand being the smallest.

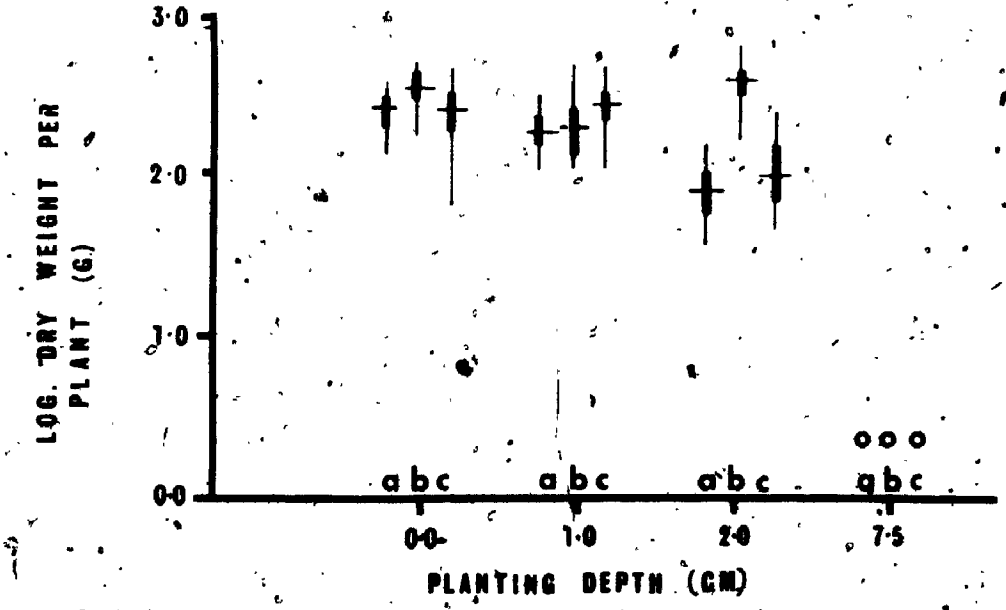
There was no clear trend in dry weights of plants with planting depth.

VI.4 Discussion and conclusions

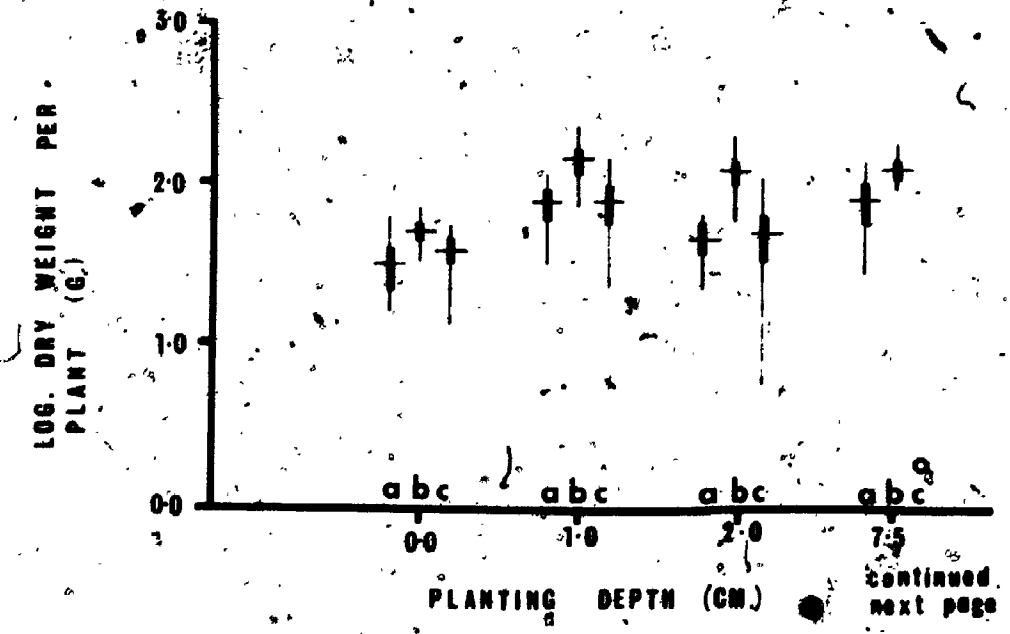
Natural selection as proposed by Darwin (1859) is particularly severe for organisms with similar requirements. Harper et al (1961) proposed that seedlings of closely related species frequently occupy "safe sites" which differ in microtopography or microclimate. The occupation of different safe sites by different species would reduce competition between them. The number and variety of safe sites in a habitat partly determine the diversity of species

FIG. VI.5 DRY WEIGHTS OF PLANTS OF P. LAPATHIFOLIUM (a), P. PENSYLVANICUM (b) AND P. PERSICARIA (c), GROWN IN FIVE SOILS FROM FOUR PLANTING DEPTHS. (Means; horizontal lines, ±1 S.E.; thick lines, ranges; thin lines).

SOIL TYPE 1 : POTTING COMPOST

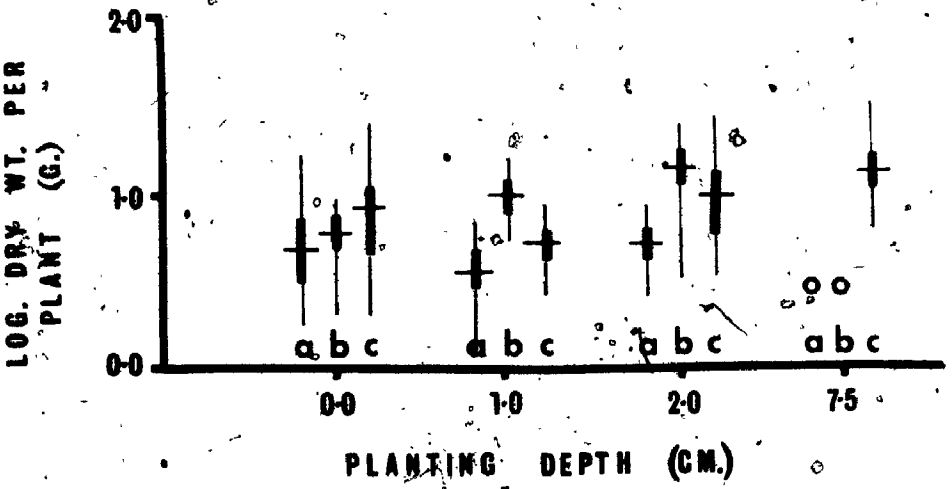


SOIL TYPE 2 : SILT, CLAY

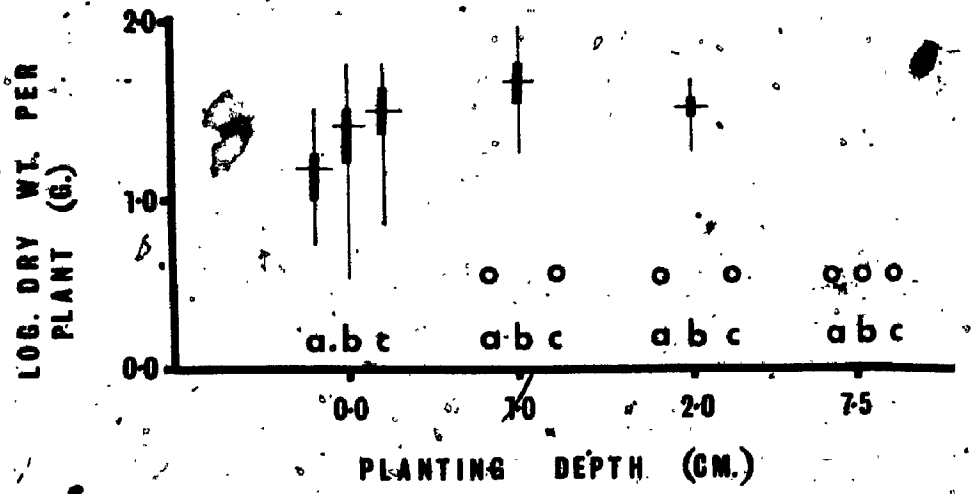


continued on next page

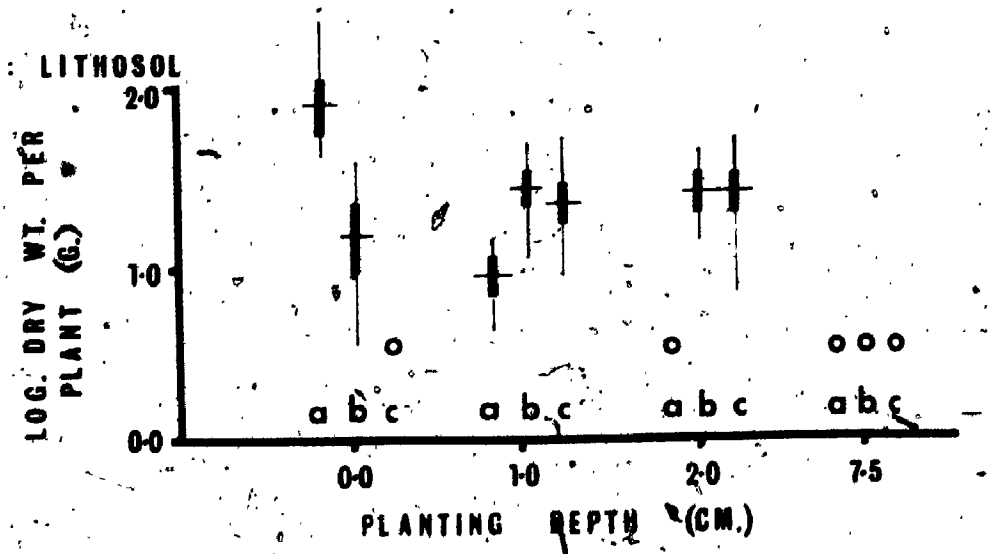
SOIL TYPE 3: SAND



SOIL TYPE 4 : GRAVEL



SOIL TYPE 5: LITHOSOL



occupying it. Sheldon (1974) showed that features of the propagule, such as morphology and physiological requirements determine the type of safe site in which germination and seedling establishment would be most successful. Seed polymorphisms or plastic variation within a species increases the number of safe site types available to that species for colonization.

Polygonum lapathifolium, P. pensylvanicum and P. persicaria frequently occur together on riverbanks. The cohabitation of these species in a small area may be explained by their occupation of different safe sites within that area. Riverbank soils (lithosols) are very heterogeneous especially in terms of water content and particle size (see Chapter II). Soil heterogeneity within a small area would provide a variety of safe sites for colonization by a number of species. The laboratory experiments described in this chapter were designed to reveal species differences with regard to emergence and establishment in different soils and water regimes.

There were very similar trends in seedling emergence for each of the three species. Good emergence was noted from drier soils. This finding is supported by field observations that flushes of seedlings appear continuously during late spring and early summer as the river level recedes and the soils begin to dry. The experiment showed that growth of very young seedlings was inhibited by submergence or waterlogging. Presumably very young seedlings in the field would cease growth temporarily should the river level rise

for a short time. All three species responded similarly to soil type, yielding higher percentages of emergence in potting compost and clay soils. There were some differences between species in emergence from various soil depths. P. lapathifolium was sensitive to burial and only emerged readily from the soil surface or 1 cm below it. The other two species were more tolerant of deeper burial.

Although germination and early establishment were cited by Sagar and Harper (1961) as the most critical stages in the life history of a plant, Miles (1972) found situations where older plants played at least as important a role in colonization as the earlier stages. Maturing plants of Polygonum spp. growing on well drained riverbank soils must be able to survive a summer shortage of soil-water before they enter the reproductive phase of their life history in late summer and autumn. If they die at this stage no achenes will be produced. For this reason, the survival of older plants was considered essential for the colonization of riverbanks.

Dry weight and height measurements for plants of each species of Polygonum differed between most soil types and between most water regimes. Seedlings of P. lapathifolium grew larger where the water table was 10.0 cm below the soil surface. They achieved maximum size when sown on the surface. The relatively small achenes (see Chapter III) would achieve closer contact with the damp soil surfaces compared with those of P. pensylvanicum, thus reducing the

than those of the other two species (for achene weights, see Chapter IV) and presumably possessed the smallest energy reserves. In P. lapathifolium, seedling anchorage may be enhanced by hook-like remains of the vascular bundles, the only portion of the decayed perianths which usually remains in the spring (see Chapter IV). Additional support for surface sown plants was created by the development of many lateral roots in seedlings which had toppled over (Fig. VI.6).

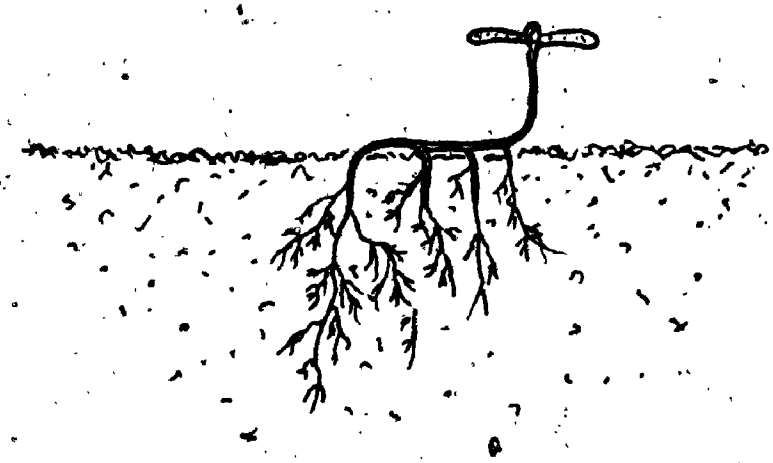


Figure VI.6 Drawing of a seedling of P. lapathifolium originally planted on the soil surface, which later toppled over and grew lateral roots above the soil level for anchorage.

Seedlings of P. pensylvanicum and P. persicaria grew largest where the water table was 18.0 cm below the soil surface. Seedlings of both species usually showed maximum growth when buried at a depth of 1 cm. Shallow burial would reduce the risk of dessication on this drier soil as compared with seedlings planted on the soil surface. Plants of all three species were smaller when planted 7.5 cm

deep, those of P. lapathifolium being particularly sensitive and failing to survive. Should a gravel bar become buried in late spring, some seedlings of P. pensylvanicum and P. persicaria would emerge and survive whereas those of P. lapathifolium would all die.

Plants grown under the wetter soil conditions tended to remain small. These plants and other small plants grown under other conditions possessed short roots which were very much branched. Plants grown in drier soils appeared to be well adapted to dry sites as these plants possessed relatively long and fibrous root systems.

The riparian soils on which the three species of Polygonum are frequently found are very heterogeneous; in some sites gravel may dominate, in others it may be clay and in a third a true lithosolic mixture may exist. Emergence, dry weight, plant size and flowering data have shown that each species has the ability to emerge, grow and flower under different conditions of soil moisture, burial depth and soil type. These differences between species suggest that competition for sites is at least partially reduced.

CHAPTER VII

SUMMARY

VII.1 Gravel bank plants

Perennial and annual plant species growing on river gravel banks exhibit fundamental differences in their strategies for surviving the severe environmental conditions which occur in this habitat between late autumn and early spring.

a) Plants of perennial species "endure" such conditions by means of strong flexible aerial parts (e.g. Salix interior) or die down to an underground stem (e.g. Phalaris arundinacea). They thereby minimize the number of plant parts exposed to such conditions. Lubke (1968) found that some gravel bank perennials (Saponaria officinalis and Silene cucubalus) showed few adaptations which could be attributed specifically to this habitat.

b) Plants of annual species "avoid" damage on gravel banks during the winter. This strategy relies on the ability of propagules (seeds) to remain viable between growing seasons and to germinate in the spring.

VII.2 The problem

The aim of this thesis (as stated in Chapter I) is to examine the biological features which allow three species of the genus Polygonum to occur frequently on gravel banks of the Thames River in the London area. Three annual species

were chosen for study since adaptations at all stages of their life cycles could be studied during the term of a Ph.D. investigation. The species were Polygonum lapathifolium L., P. pensylvanicum L. and P. persicaria L.

The procedure was as follows:

1. Information concerning the gravel bank environment was obtained by means of surveys and published data. These data were used to elucidate unusual attributes of this habitat which would usually be considered as inhospitable to the growth and survival of most plants.
2. The distribution of each of the study species was examined by means of surveys, within both gravel banks and neighbouring habitats. This information was used to identify the habitats or features of them with which each species was associated.
3. Achene dispersal, germination and seedling establishment were considered critical life history stages as they coincided with periods of extreme conditions on gravel banks. These three stages were examined under field and simulated environmental conditions to identify features which might contribute to success at each stage under gravel bank conditions. Such adaptations were compared between species. The contributions of each adaptation to the success of each species in this habitat was discussed.

VII.3 The gravel bank habitat

The soil type of this habitat was identified as a

lithosol (stony with undefined horizons and a matrix of various sized particles), and found to be extremely porous. The porous nature of this substrate allowed rapid and thorough drying when the gravel banks and bars were exposed as the river levels fell during the late spring and summer. The river levels were high during the autumn, winter and spring, thus during this period the banks and bars become waterlogged and often submerged for several months. The nutrient status of these porous soils was low, but the pH was high due to the predominance of calcium carbonate in the rocky particle fraction of the soil. The results of soil chemical tests confirmed those of Lubke (1968) who studied these and other gravel banks in the vicinity of London.

VII.4 Distributions of the study species.

Surveys provided much new information concerning distributions and habitat associations for each species. The interpretation of distribution data could only be made when used in conjunction with data obtained from experimental studies. An ambiguity of interpretation often arose when a species was recorded as absent at a particular site. It was not known whether this absence was due to limitations of dispersal, unfavourable environmental conditions or incomplete records at that site. Such a problem was solved by means of subsequent experimental studies.

Each of the three species occurred with some regularity on the gravel banks of the Thames River, although P. persicaria was relatively infrequent. This species was commonly found as a weed in agricultural land. Its presence on gravel banks may have been the result of accidental introductions of achenes in the faeces of herbivorous mammals or the achenes (which are buoyant) may have been washed from agricultural land with water run-off. The relative rarity of this species and the poor survival of achenes in wet soils suggest that P. persicaria may have to be introduced repeatedly to gravel banks for continued survival in this habitat.

Plants of P. lapathifolium and P. pensylvanicum were frequent in all parts of gravel banks. The former species produced a greater biomass in low or wet areas than P. pensylvanicum which produced a greater biomass in the higher and drier sections. This apparent difference in microsite adaptation would reduce competition between these species in the drier and wetter parts of gravel banks. It may be argued that such results indicated the occurrence of competitive stress between the two species with the result that each grew largest in different sites. This was not the entire cause of differential biomass production because growth experiments (in which competition was kept to a minimum) also showed that maximum biomass for P. lapathifolium was achieved on slightly wetter soils than was the case for P. pensylvanicum. Such differences in microsite adaptation

have also been demonstrated by Harper and Sagar (1953) in explaining the co-existence of three closely related species of Ranunculus in a permanent pasture. Their results showed that variable microtopography and drainage features partly accounted for the continued survival of the three species in this habitat.

P. pensylvanicum reaches its northern limits in southern Ontario where it is apparently restricted to the light soils of gravel banks and shorelines (except in extreme southwestern Ontario). Further to the south, this species is more typically associated with arable land where it is often a serious weed.

P. lapathifolium was found on riverbanks and lake shorelines throughout Ontario. This species was found only occasionally as an agricultural weed in this province. Perhaps only P. lapathifolium may be called a primarily wetland species, the other two species being more frequently associated with other habitats over the main part of their ranges. Nevertheless, all three species may be found on gravel banks near London, Ontario.

VII.5 Adaptations to the gravel bank habitat

VII.5.1 The dispersal stage

The degree to which a dispersal unit or diaspore is adapted to specific dispersal agents, ranges from no morphological or physiological adaptations (usually small diaspores) to examples where they are so specific to

particular dispersal agents, that the rarity of the agent in one season may jeopardize the survival of the species.

The dispersal process consists of several stages. The diaspores may show adaptive features at each stage. The first stage is the picking up of the diaspore by the dispersal agent (adaptive features at this stage may include attractants for animals, the timing of seed fall etc.). Once picked up by the agent, the diaspore must be carried for a distance in a viable state (adaptations for this stage include the many kinds of morphological structures associated with diaspores). The third and last stage is the deposition of the still viable diaspore in a site suitable for growth. Dispersal is a complex process which depends on success in all three stages if the process as a whole is to be successful.

Recent literature concerning dispersal is sparse. Ridley (1930) collated many listings and reports of possible dispersal methods of various species. Very little experimental work has been published for the species discussed here. Field observations in the London area have revealed two methods which enable dispersal of these species to, from and within gravel banks. The field observations were followed by a series of experimental studies.

The first dispersal agent studied was river water. The achenes fell from the parent plant onto the gravel bar prior to the autumn rise in river water levels which picked up the achenes from the gravel banks and floated them

downstream. The achenes of each species were capable of floating for periods of time determined by the amount of water turbulence, the condition of the achenes and its enveloping perianth and the size of the achene (largest in P. pensylvanicum, smallest in P. lapathifolium. Achenes of P. lapathifolium floated for longer durations than those of P. pensylvanicum. Water dispersal (hydrochory) was believed to be a highly adaptive feature in these species. Examination of each stage of this dispersal method revealed further adaptations:

1. The timing of achene shedding coincided with the maximum possibility of being picked up by the dispersal agent (autumn floods).
2. After falling from the parent plants and prior to water dispersal the perianth segments dried while the diaspores lay on the gravel. Dry perianth segments permitted the diaspore to float longer.
3. Usually the perianth segments remain attached until the achenes had germinated. Their presence on the achenes in the dispersal stage was essential. Each segment was closely wrapped around the achene forming a sac containing a small amount of air which conferred buoyancy on the diaspore. Sinking only occurred after these segments eventually became separated from each other during prolonged water turbulence.
4. The viability of diaspores was not altered by the vector during transportation. Achene dormancy was weakened

during dispersal by water in P. lapathifolium but strengthened in the other species. The adaptive value of this response was not obvious and would seem to have little effect in Ontario, since autumn temperatures would prevent germination in P. lapathifolium and achenes of all species would be capable of germinating in spring after prolonged low winter temperatures. Perhaps this phenomenon might be more important after any spring water dispersal had taken place. This result was intriguing and required further study before an adequate explanation could be given. It may be very important in explaining why the three species can co-exist in a gravel bank habitat.

5. Hydrochory ended with the beaching or sinking of diaspores. Water carried the diaspores to similar and potentially colonizable habitats; this is a critical feature of a suitable agent. Achenes that sank could be further dispersed by water currents and if they eventually were deposited on the river bed would remain viable for many months (except those of P. persicaria) until brought to the surface by a change in water course, a lowering of the water level or gravel movements. Sinking after short-distance dispersal may be an adaptive feature of hydrochorous diaspores since it prevents eventual transportation to large bodies of water, such as lakes, seas or oceans.

The second means of dispersal studied was internal

animal transport (endozoochory). Field studies showed that the achenes of P. lapathifolium, P. pensylvanicum and P. persicaria were attractive to cottontail rabbits as food and a small percentage were deposited in a viable state with the faeces. Only small achenes escaped destruction by mastication, none of the large achenes of P. pensylvanicum was viable after ingestion, reflecting a strong selection factor for small achenes both within and between species. The plants of P. lapathifolium and P. persicaria appeared to be well adapted to this type of dispersal for the following reasons:

1. The timing of fruit set coincided with the movement of cottontails on and between gravel bank habitats.
2. The achenes were conspicuous at the time of maturity. The bright pink perianth segments contrasted with the dark colours of the achenes. Vivid colours of potentially endozoochorous diaspores can be a "signal" to animal dispersal agents indicating the presence of food (in the form of ripe diaspores). This phenomenon has been described by van der Pijl (1969) for other species.
3. Plants of Polygonum possessed many glands (some being odoriferous) which may have functioned as attractants to cottontails.
4. Achenes possessed large quantities of nutrients, desirable as food to many animals. The nutrient status of smartweed achenes is high (Potts 1970).

5. The fruit wall of each achene was thick, hard and smooth. These qualities protected the enclosed embryo and endosperm of some achenes during passage through the digestive tract. Observations suggested that the embryo was only vulnerable if the fruit wall was damaged during mastication. If this happened the entire achene contents were digested and empty fruit wall fragments were deposited in the faeces.
6. Viable achenes were deposited with the faeces. Achenes which germinated in faeces in the greenhouse produced vigorous seedlings. On gravel banks, germinating achenes in faecal pellets would be in close contact with organic material (which has a better water holding capacity than loose gravel) and nutrients.

The plants of each species appeared to be well adapted to these two types of dispersal (except endozoochory in P. pensylvanicum). A further consideration is that water is a unidirectional agent, dispersing propagules downstream only. This dispersal method can be complemented by endozoochory (except in P. pensylvanicum) which permits colonization in other directions. Since achenes of P. pensylvanicum could be dispersed by water but not by cottontails this may have accounted for the restricted distribution (i.e. to riverbanks and bars) of this species in the London area. A second consideration was that colonization of a new site may be accomplished by one original diaspore. Mulligan and Findlay (1970) have shown that plants of all three species are capable

of self-fertilization. Baker (1955) suggested that self-fertilization is an adaptive feature of colonizing species.

VII.5.2 The achene dormancy and germination phase

For gravel bank annuals, the state of propagule dormancy is important for several reasons:

1. As a propagule, the plant is in a form in which physiological requirements from and physical contact with the environment are minimal. For this reason the risk of physical and physiological damage is reduced. This is important during dispersal and for survival during severe climatic and habitat conditions.
2. While the seeds are dormant various events important to the plant occur (e.g. dispersal, embryo ripening etc.).
3. Most propagules which exhibit dormancy, will germinate only when environmental conditions become suitable for both germination and subsequent seedling growth.

Freshly matured achenes of all three species possessed an innate dormancy which was broken by prolonged periods at low temperatures. Such a mechanism ensured that germination did not occur during the year that the achenes were produced, an event which would have been followed by total seedling mortality during the winter. Achenes, which had been after-ripened by subjecting them to low temperatures, germinated readily in a warm, moist environment; however, when they were buried or submerged a state of enforced dormancy occurred. Burial or submergence of achenes by lithosol movements must be a frequent occurrence in gravel bank habitats. Achenes

of P. lapathifolium and P. pensylvanicum which had been enduring enforced dormancy germinated after being brought to the soil surface or after flood waters receded. In contrast, most achenes of P. persicaria lost viability during storage in wet sites and thus were not well adapted to riverbank habitats. Achene dormancy in P. lapathifolium and P. pensylvanicum was seen as an adaptation which enabled dispersal and survival of plants during unfavourable periods of growth.

VII.5.3 Seedling establishment and early growth

Seedling establishment and early growth were considered critical parts of the life history on gravel banks. During late spring, when most seedlings emerge in the field, river levels fluctuate considerably resulting in frequent flooding, burial and erosion of the habitat. The lithosolic soils are very porous and become exceedingly dry as the river levels fall in the summer. Survival of seedlings in this habitat is dependent upon adaptations to these environmental events.

Germinated achenes entered a state of slow or no growth when waterlogging or submergence occurred and normal growth was only resumed when the soils became drier. By means of reduced growth rates such seedlings were adapted to avoid damage by water currents during temporary spring flooding. At this time sedimentation and erosion were frequent events. Burial (up to 7.5 cm) of germinated achenes of P. pensylvanicum and P. persicaria did not cause high seedling mortality;

however, seedlings of P. lapathifolium were very susceptible to burial and in most soil types showed considerable seedling mortality if buried by more than 1 cm of soil. Seedlings of P. pensylvanicum and P. persicaria grew largest in drier soils while those of P. lapathifolium achieved a maximum growth in wetter situations. This result was noted in field surveys and was confirmed by experimentation. It suggested a slightly different habitat requirement for P. lapathifolium. Seedlings of all three species rapidly produced deep root systems, especially in drier soils, an adaptation which allowed the survival of plants in soils with deep water tables (e.g. gravel banks in the summer).

LIST OF APPENDICES

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Appendix I. Taxonomy of Polygonum lapathifolium, P. pensylvanicum and P. persicaria.

Introduction

Self-compatibility has been shown to be a characteristic of annual Canadian weeds (Mulligan and Findlay 1970). This breeding mechanism perpetuates the production of the best adapted genotypes for various micro-environments (Allard and Hansche 1965). In this way a number of different micro-environments within one habitat may be utilised by different genotypes as Gadgil and Solbrig (1972) have shown with the parthenogenetic biotypes of Taraxacum officinale L. New habitats may be exploited which enlarge the range of the species. This mating type also enables the production of viable seeds after long distance dispersal in the absence of pollinators or other plants (Baker 1955). While numerous intraspecific self-pollinating biotypes are a criterion of successful colonization in many species, their existence has been the cause of much taxonomic confusion.

The species; Polygonum lapathifolium L. (pale smartweed, renouée a feuilles de patience), P. pensylvanicum L., (pink smartweed, Pennsylvania smartweed, renouée de pennsylvanie) and P. persicaria L. (persicaria, lady's thumb, renouée persicaire) are taxonomically closely related but are separated from each other by several constant factors. Hybridization is very rare but has been reported between P. lapathifolium and P. persicaria (Stanford 1925a, Timson 1965a). Selfing is reported to be the most frequent pollination method

(Mulligan and Findlay 1970). Timson (1963) has identified self pollination in P. lapathifolium as being responsible for the existence of many phenotypes, each possessing a set of characters which are more or less constant from one generation to the next.

a) Polygonum lapathifolium

Much taxonomic work has been done in Europe which has a bearing on the situation in North America. The approaches have been, on one extreme, not to divide the species at all (Timson 1963) and on the other extreme to name every variant.

Timson (1963) recognizes that much of the variability within the "species" (in the widest sense) is due to the existence of perpetuating, self-pollinating biotypes. On this basis, he suggests that the species should not be subdivided as the occasional occurrence of cross-pollination has and will continue to create a diverse range of intermediate forms.

Other authors have described two common taxa. One characteristically possessing small achenes; long, slender, drooping inflorescences; pink flowers and glabrous leaves. The other taxon having achenes greater than 2 mm. long, a stout inflorescence, green flowers and a tomentum (white downiness) on the lower surfaces of the leaves. The flower has been frequently named P. nodosum Pers. or P. petecticale Druce. The other taxon has usually been named P. lapathifolium L. (eg. by Tutin, 1952) or P. tomentosum Schr. Tutin (1952) and Britton (1933) have regarded these principle taxa as

species. Danser (1921) and Schuster (1906) gave the taxa subspecific status describing complex hierarchies and naming many intermediate types and varieties.

In North America, descriptions of the taxonomy of P. lapathifolium have been equally confusing. Small (1895) distinguished two taxa at the specific level. P. lapathifolium L. was distinguished from P. incarnatum Ell. on achene shape, flower colour and style form. Within his concept of P. lapathifolium L., he distinguished two varieties, namely P. lapathifolium incanum (Schmidt) Koch and P. lapathifolium nodosum (Persoon) Small. These have the same characteristics as the principle European taxa, i.e. P. tomentosum Schr. and P. nodosum Pers. and are probably synonomous.

Irigoyen and Thellung (1929) applied the nomenclature of Danser (1921) to North American taxa, recognizing P. lapathifolium nodosum and P. lapathifolium tomentosum as the principle varieties, P. lapathifolium mesomorphum as the main intermediate and naming fifteen varieties and other intermediate types of these.

In Europe at the present time (an exception being Timson 1963) the name P. lapathifolium L. is reserved for the taxon with large seeds, green flowers, erect inflorescences and tomentose leaf undersurfaces, and the name P. nodosum Pers. for the small seeded pink flowered, lax inflorescenced, glabrous taxon. Fernald (1921) suggested that in Linnaeus' description of the species, P. lapathifolium more aptly described P. nodosum Pers. Since 1921, in North America,

P. lapathifolium L. has usually been regarded as being synonomous with P. nodosum of Europe and not with the European P. lapathifolium L. P. lapathifolium of most European authors has usually been named P. scabrum Moench. in North America.

In North America two important sources of confusion have arisen;

(a) Synonomy. This has been further complicated by the same name, i.e. P. lapathifolium L. being adopted by widely used floras (Tutin 1952; Fernald 1950) for different taxa.

(b) The status of P. lapathifolium L. and P. scabrum Moench. Various contemporary authors recognize them as species, varieties or merely self-perpetuating lines of the same species.

Most herbarium specimens in Ontario have been identified according to taxonomic keys of "Gray's Manual of Botany" (Fernald 1950). According to Fernald (1950) there are two species, P. lapathifolium L. which has three varieties in eastern North America, and P. scabrum Moench. Both of these taxa have been included within the broad definition of P. lapathifolium L. given by Timson (1963). In allowing the two taxa specific status, Fernald (1950) indicated that the two species are very closely related. For these reasons and for the sake of convenience the discussion of P. scabrum is included in this account within P. lapathifolium "sensuo lato". Fernald (1950) distinguished P. lapathifolium from P. scabrum using the following characters.

"Spikes pink or purplish, paniculate, erect, arching or pendulous, on definite glabrous to sparsely glandular peduncles, 1-8 cm. long; mature calyx ovoid to rhomboid, constricted toward summit to form a thick beak overtopping achene; achene 1.8-2.2 mm. long, 1.5-2.0 mm. broad.
P. lapathifolium L.
(includes P. nodosum Pers. and P. incarnatum Ell.)

Spikes green (exceptionally purplish), subcarymbosely paniculate or sessile on spiciform erect branches, erect or nearly so, 1-5 cm. long; axis copiously glandular; mature calyx round- to ovoid, gradually rounded at summit, about equally or slightly shorter than achene; achene 2.5-3.5 mm. long, 2.3-2.8 mm. broad.
P. scabrum Moench
(Syn; P. persicaria spp. tomentosum Schrank.)"

The ranges of both of these taxa include Ontario. Boivin (1967) has also listed P. lapathifolium L. and P. scabrum Moench. as Ontario species. Within P. lapathifolium (as defined by Fernald 1921), the "typical" form, var. prostratum Wimm. and var. salicifolium Sibth. have been stated to occur in Ontario. These taxa differ in the following characters.

"(a) Leaves lanceolate, broadest near base, attenuate to tip.

(b) Leaves green on both surfaces except for sessile glands beneath, up to 2.5 cm. long and 5 cm. broad; longer spikes arching to pendulous, 2-8 cm. long
P. lapathifolium L. "Typical"

(b) Leaves white pubescent beneath, narrowly lanceolate, the longer 3-10 mm. wide; spikes 1-few, erect, 1-3.5 cm. long.
var. salicifolium Sibth.
(Syn. var. incanum (Willd.) W.D.J. Koch; P. tomentosum, var. incanum sensu ed. 7 Robinson and Fernald 1908)

(a) Leaves elliptical, oblong - ovate or subrhombic, broadest well above base or near middle, not long attenuate.

(c) Prostrate or depressed, the trailing and much - forked branches 1-4.5 dm. long; leaves subrhombic, cuneate at base, firm, often with large purple blotch above, the principal ones 2.5-7 cm. long and 1.5-3.5 cm. broad; spikes 1-4 cm. long.
var. prostratum Wimm."

Gleason and Cronquist (1963) recognized one very variable species (P. lapathifolium L.) which has two varieties (var. lapathifolium and var. incanum (Roth) K. Koch) both occurring in Ontario. Of the characters given for this species, the following are relevant to this discussion.

"Erect or occasionally; lvs variable, commonly lanceolate and acuminate, often tomentose beneath; racemes numerous, nodding, 1-5 cm. ....., col rose, white or green, ... achene ....., 1.7-3.2 mm., 75-90% as wide.
P. lapathifolium L."

The following characters distinguish the two varieties.

"... glabrous or nearly so at maturity except commonly for some glands on the lower leaf surface, a few glands also occasionally on the peduncle and axis of the infl., the achenes are rarely over 2.2 mm.
var. lapathifolium.

... leaves more or less tomentose beneath, and the summit of the peduncle and axis of the infl. densely glandular; the achenes are seldom under 2.5 mm.
var. incanum (Roth) K. Koch
(Syn. P. tomentosum; P. scabrum)"

P. scabrum Moench. and P. lapathifolium var. salicifolium Sibth. listed by Fernald (1950) are clearly included in var. incanum as listed by Gleason and Cronquist (1963). Timson (1963) determined the reliability of characters frequently

used in taxonomic keys, by cultivation experiments. He determined that leaf tomentum and perianth anthocyanin are "critical characters", not varying between individual plants and constant in cultivation. Leaf shape, seed size and shape did not vary significantly between the taxa used in his experiments.

b) Polygonum pensylvanicum L.

P. pensylvanicum produces large quantities of nectar, the flowers which open on sunny days are particularly attractive to bees. Knuth (1906) described a pollination mechanism characteristic of many species of Polygonum, in which the stamens curve in and deposit pollen on the stigma of the same flower if no previous pollination has occurred. This mechanism probably also operates in P. pensylvanicum. The frequency with which insects visit the flowers suggests that autogamic lines may not be as discrete as in P. lapathifolium where the taxonomy is far more complex.

On the basis of habit, leaf pubescence, calyx size, achene size and glands on the peduncles, Fernald (1950) described the typical taxon and five varieties. The "typical" taxon and var. laevigatum Fern. are listed as occurring in Ontario, each of these has a pale form. Forma pallescens Stanford is included in this key, whilst not listed by Fernald (1950), it is commonly found in identifications of appropriate specimens in Ontario herbaria, it was described in detail by Stanford (1925b). Soper (1949) records the variety eglandulosum J. C. Myers as occurring in the southern

Ontario peninsula. Fernald (1950) used the following characters to identify the Ontario taxa.

"a. Leaves evidently strigose, lanceolate .....b.

b. Peduncles covered with spreading gland-tipped hairs; stamens (6-)8. Calyx 3-4 mm. long; achene 3.3.5 mm. long, 2.2-2.8 mm. broad
P. pensylvanicum "typical"
Syn. var. genuinum Fernald (1917)
flowers white forma albinum Fern.

a. Leaves smooth and glabrous or promptly glabrescent; achenes 2.5-3.5 mm. broad .....c.

c. Peduncles and axis of inflorescence copiously stipitate-glandular. Stem erect, ascending or depressed; leaves lanceolate to narrowly lanceolate, acuminate; the principle ones 0.5-2 dm. long; spikes mostly peduncled, the larger ones cylindric, 2-5 cm. long; stamens 7-8.
var. leavigatum Fern.
Leaves and flowers pale forma albineum Farw.
Colourless glands forma pallescens Stanford

c. Peduncles and axis of inflorescence glabrous
var. eglandulosum J. C. Myers."

Boivin (1967) listed the above three varieties and forma albineum as native to Ontario. Gleason and Cronquist (1963) recognized two varieties of Polygonum pensylvanicum L. in the eastern United States and adjacent Canada. Only one of these, var. pensylvanicum occurs in Ontario and this includes all of the predescribed varieties and forms of Fernald (1950).

c) Polygonum persicaria L.

Fernald (1950) listed two forms and two varieties within this species. Boivin (1967) and Gleason and Cronquist (1963) record neither forms nor varieties.

Forma submersa Erikson; an inundated form, having thin pellucid leaves.

Forma albiflora Millsp.; has white flowers.

var. augustifolia Beck; has narrow leaves (3-5 mm.) which are strigose on both surfaces. The range of this variety does not include Ontario, but occurs as close as New York State, according to Fernald (1950).

var. ruderale (Salisb.) Meisn.; this variety appears to be very close to the typical form. Characters used by Fernald (1950) in it's separation from the typical taxon are: habit; prostrate, depressed, much branched (typical form: ascending or decumbent stem, simple or branched), primary leaves; 2-5 cm. long (typical: 3-15 cm. long), inflorescence; subglobose to cylindric 0.5-1.5 cm. long (typical: oblong or thick cylindric, leading ones 1.5-4.5 cm.).

Appendix II.1a. References used for the construction of world distribution maps of P. lapathifolium, P. pensylvanicum and P. persicaria (Figures II.1 to II.3). Only references containing reports indicating positive occurrence of the study species are listed in this Appendix (see Appendix II.1b for other references used for world distribution maps).

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Appendix II.1.b References used for the construction of world distribution maps of P. lapathifolium, P. pensylvanicum and P. persicaria (Figures II.1 to 3). References given below made no reference to the occurrence of the study species within the areas covered. (References are given in a concise form in order to save space.)

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Appendix II.2

a) Summarized results for the analyses on frequency data for P. persicaria on three soil types and two land uses near London, Ontario. Information statistic was used in these analyses and "Yates correlation for continuity" was applied where required.

Data from Survey IIIa, Chapter II.

Source of Information	D.F.	
R x C test for independence of land use and soil type	2	7.066 *
Pairwise comparisons by STP		
clay x loam	1	0.030 ns
clay x sand	1	13.780 *
loam x sand	1	3.728 ns
agricultural land x wasteland	1	7.066 *

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

STP Simultaneous testing procedure (Sokal and Rohlf 1969)

Appendix II.2 (Continued)

b) Summarized results for a test of linear proportions (Snedecor and Cochran 1967) to test the hypothesis that there is a linear increase in the proportion of occurrences for P. persicaria in agricultural land as one moves from sandy through loam to clay soils.

	sandy soil	loam	clay soil	total
agricultural land (a)	9	24	28	61
wasteland	25	24	24	73
total (n)	34	48	52	134
proportion (p) = a/n	0.2647	0.5000	0.5385	0.4552

score x	1	2	3

Regression coefficient (b)	S.E. of (b)=(s)	normal deviate (b/s)=(Z)	Probability (P)
0.1293	0.05477	2.3608	0.0182*

We accept the null hypothesis, i.e. that there is a linear increase in the proportion of occurrences for P. persicaria on agricultural land as one moves from sandy soils through loam to clay soils.

Appendix II.3

Summarized results for the analysis on frequency data for P. persicaria in five crop types (corn, small grained cereals, pasture, tobacco, others). Information statistic was used to compare presence and absence data for all sites. Data from Survey IIIa, Chapter II.

Source of Information	D.F.	Information
R x C test for independence of crop types	4	124.834 *
Crop comparisons using STP		
corn, tobacco, pasture	2	5.991 ns
corn, tobacco, pasture, others	3	6.370 ns
small grained cereals, corn	1	7.392 *

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

STP simultaneous testing procedure (Sokal and Rohlf 1969)

Appendix II.4

Summarized results of information analyses on frequency data for presence/absence of three species of Polygonum in 300 riverbank sites, near London, Ontario. Data from Survey IIIb, Chapter II.

Source of Information	D.F.	Information
R x C test for independence of species presence and species absence	2	32.48 *
Pairwise comparisons by STP		
P. lapathifolium x P. pensylvanicum	1	11.890 *
P. lapathifolium x P. persicaria	1	30.452 *
P. pensylvanicum x P. persicaria	1	4.864 *

* significant ($P < 0.05$)

STP simultaneous testing procedure

Appendix II.6

Species and their frequencies from 60 quadrats (1 m. x 1 m.) located on gravel bars along the Thames River, London, Ontario. (Species nomenclature taken from Gleason and Cronquist 1963)

Abutilon theophraste Medic.	1
Acalypha rhomboidea Raf.	4
Acer negundo L.	7
Achillea millefolium L.	1
Agropyron repens (L.) Beauv.	4
Agrostis stolonifera L.	36
Alisma subcordatum Raf.	1
Alliaria officinalis Andrz.	3
Amaranthus graecizans L.	1
Amaranthus retroflexus L.	4
Ambrosia artemisiifolia L.	12
Ambrosia trifida L.	5
Arctium minus Schk.	9
Asclepias incarnata L.	1
Aster spp. (vegetative)	2
Atriplex patula L.	1
Barbarea vulgaris R.Br.	32
Bidens cernua L.	19
Bidens frondosa L.	4
Brassica kaber (DC.) L. Wheeler	2
Bromus inermis Leyss.	1
Chaenorrhinum minus (L.) Lange	11
Chenopodium album L.	17
Chenopodium glaucum L.	2
Chrysanthemum leucanthemum L.	4
Cirsium vulgare (Savi) Tenore	2
Convolvulus sepium L.	1
Conyza canadensis (L.) Cronq.	3
Crataegus sp. (seedling)	1
Cyperaceae (vegetative)	16
Cyperus esculentus L.	10
Cyperus rivularis Kunth	7
Dactylis glomerata L.	4
Daucus carota L.	10
Digitaria ischaemum (Schreb.) Muhl	1
Digitaria sanguinalis (L.) Scop.	5
Echinochloa crugalli (L.) Beauv.	32
Echinocystis lobata (Michx.) T&G	4
Echium vulgare L.	2

Appendix II.7

Results of analyses used on the data in Survey IV, Chapter II to determine similarities and differences in dry weight of plants of a) P. lapathifolium between quadrat group and b) P. pensylvanicum between quadrat group.

a) P. lapathifolium

Results of analysis of variance of plant weights from 5 quadrat groups.

Source of variation	D.F.	S.S.	M.S.	F_s
Among groups	4	11171.9	2792.9	2.8266 *
Within groups (Error)	35	34583.1	988.0	
Total	39	45755.0		

$\chi^2_{0.05(4)}$ = 14.860 (given) χ^2 = 13.582

Results of Student - Newman - Keuls test for comparison of mean based on unequal sample sizes.

Quadrat group	B	C	E	A	D
Mean value for dry wt. (g.)	12.4	17.5	21.3	25.8	64.5

Values underscored by a common line are not significantly different from each other (P > 0.05)

Appendix II.5 (Continued)

Poa annua L.	1
Poa compressa L.	8
Polygonum aviculare L.	17
Polygonum convolvulus L.	3
Polygonum hydropiper L.	34
Polygonum lapathifolium L.	42
Polygonum pensylvanicum L.	37
Polygonum persicaria L.	9
Populus deltoides Marsh	8
Populus spp. (seedlings)	14
Potentilla anserina L.	3
Ranunculus repens L.	2
Rorripa islandica (Oeder) Borbas	3
Rorripa sylvestris (L.) Besser	2
Rumex crispus L.	9
Rumex obtusifolius L.	3
Salix amygdaloides Anderss.	1
Salix interior Rowlee	25
Salix pyrifolia Anderss.	1
Salix rigida Muhl.	21
Salsola kali L.	1
Saponaria officinalis L.	22
Scirpus validus Vahl.	1
Scrophularia marilandica L.	1
Scutellaria galericulata L.	1
Setaria viridis (L.) Beauv.	17
Silene cucubalus Wibel.	7
Sisymbrium officinale (L.) Scop.	7
Solanum dulcamara L.	5
Solanum nigrum L.	4
Solidago bicolor L.	1
Solidago canadensis L.	4
Solidago spp. (vegetative)	7
Sporobolus neglectus Nash.	2
Stellaria aquatica (L.) Scop.	10
Stellaria media (L.) Cyrill.	22
Taraxacum officinale Weber	7
Trifolium hybridum L.	3
Trifolium pratense L.	1
Trifolium repens L.	13
Urtica dioica L.	2
Verbascum thapsus L.	5
Verbena hastata L.	23
Verbena spp. (vegetative)	32
Verbena urticifolia L.	26
Veronica serpyllifolia L.	3
Vitis riparia Michx.	1
Xanthium strumarium L.	7

Appendix II.6

Data gathered in Survey IV, Chapter II pertaining to descriptions of 60 quadrats which were located on gravel banks and described by 19 attributes. For descriptions of sampling and data collection see the description of Survey IV in Chapter II. (+) Dry weight values measured to the nearest gram. The value (0) indicates that plants were present but had a total dry weight <0.5 g. and the symbol (-) indicates absence of plants. (*) Attributes not included in the ordination or classification described in Chapter II.

\+ 1. Dry weights of plant material (g.) per quadrat (1 m^2.) excluding the dry weights of the study species.

424	759	463	185	238	610	938	649	438	770
650	348	202	74	166	125	126	237	148	948
266	755	998	772	122	889	614	982	517	242
207	224	33	106	191	215	58	825	33	783
594	178	389	464	249	86	478	170	193	459
60	244	195	143	270	420	108	159	315	496

2. Number of plant species per quadrat.

31	35	35	35	33	31	31	31	19	36
35	39	19	19	34	23	41	37	28	38
24	14	15	19	21	24	16	18	27	17
28	15	8	9	12	5	2	4	7	27
29	14	13	31	22	10	22	10	7	27
6	20	9	11	10	26	17	7	25	23

Appendix II.6 (Continued)

3. Vertical height (m.) of quadrats above river level.

0.1	0.2	0.1	0.1	0.1	0.2	0.3	0.3	0.1	0.8
0.1	0.2	0.1	0.6	0.7	1.1	0.5	0.6	0.6	0.9
0.2	0.4	0.6	0.5	0.6	0.6	0.1	0.3	0.2	0.1
0.2	0.2	0.7	0.6	0.6	1.0	0.9	0.9	0.9	0.6
1.1	0.5	1.1	0.9	0.9	0.4	0.8	0.5	0.5	1.2
0.8	1.0	0.9	1.1	1.1	1.4	1.0	0.4	1.0	1.1

4. Horizontal distances (m.) of quadrats from river's edge.

1.5	2.5	2.5	4.5	4.5	5.5	6.5	7.5	9.5	10.5
10.5	11.5	11.5	13.5	14.5	15.5	15.5	16.5	16.5	18.5
0.5	1.5	2.4	2.5	3.4	4.5	7.5	7.5	8.5	9.5
12.5	13.5	14.5	14.5	14.5	15.5	16.5	17.5	19.5	19.5
4.5	0.2	2.3	1.2	3.4	0.3	1.3	0.2	0.2	2.2
4.4	3.4	4.4	4.4	4.4	3.2	4.4	0.3	1.2	3.3

* 5. pH of soil in each quadrat.

8.0	8.0	8.0	8.0	8.0	8.0	7.5	7.5	8.0	8.0
8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	7.5
8.0	8.0	7.5	8.0	8.0	8.0	8.0	8.0	8.0	8.0
8.0	8.0	8.0	8.0	8.0	7.5	8.0	8.0	8.0	7.5
8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0
8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	7.5

Appendix II.6 (Continued)

* 6. Phosphorus contents of soils (on a scale from 1 = very low to 5 = very high).

1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	2
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1

7. Potassium contents of soils. (scale 1 to 5 as in part 6)

2	2	3	1	1	2	2	2	1	2
2	1	1	2	1	2	2	2	2	2
1	4	2	3	2	2	2	2	2	2
1	2	2	2	2	1	1	3	1	2
1	2	2	2	2	2	2	2	2	2
1	2	2	1	2	2	2	2	4	2

* 8. Calcium contents of soils. (scale 1 to 5 as in part 6)

5	5	5	5	5	5	5	5	5	5
5	5	5	5	5	5	5	5	5	5
5	5	5	5	5	5	5	5	5	5
5	5	5	5	5	5	5	5	3	5
5	5	5	5	5	5	5	5	5	5
5	5	5	5	5	5	5	5	5	5

Appendix II.6 (Continued)

9. Nitrate contents of soils. (scale 1 to 5 as in part 6)

1	2	2	1	1	2	2	1	1	2
2	2	2	2	1	1	1	1	1	2
2	2	1	2	2	1	1	1	1	1
1	2	2	3	1	2	2	5	1	2
1	1	1	1	2	1	1	1	2	1
1	2	2	1	2	1	2	1	1	1

10. Ammonium contents of soils. (score 1 to 5 as in part 6)

2	2	3	1	2	2	3	2	2	2
2	2	2	2	2	2	1	2	2	2
5	3	2	2	2	2	2	3	2	2
2	2	2	2	2	2	2	2	2	2
2	2	2	2	2	3	2	2	2	1
1	2	2	2	2	2	2	2	3	2

11. Sulphate contents of soils. (score 1 to 5 as in part 6)

1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	1	3
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1

Appendix II.6 (Continued)

* 12. Chloride contents of soils. (score 1 to 5 as in part 6)

1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1

13. Water content of soils (% by weight).

13	19	23	20	29	14	9	27	7	4
9	4	6	2	4	6	5	2	6	3
13	4	4	4	3	6	8	14	4	4
8	3	3	12	5	3	4	3	3	3
11	12	8	6	4	8	5	15	10	4
2	3	2	2	3	5	3	10	8	7

14. "Gravel" contents of soils (% of weight).

60	7	2	22	20	26	34	3	40	51
20	25	48	46	36	58	11	30	42	9
79	82	61	77	65	62	65	44	73	67
63	83	77	58	50	59	42	16	0	2
42	58	20	52	62	67	54	60	70	70
73	66	71	72	69	67	72	54	43	51

Appendix II.6 (Continued)

15. "Sand" contents of soils (% by weight).

26	64	50	41	30	50	51	53	51	44
70	70	45	51	54	35	75	66	51	84
8	13	34	18	31	30	26	41	23	28
28	13	19	29	44	37	53	79	96	94
45	30	71	41	33	25	40	25	19	25
25	31	27	25	27	28	24	35	47	41

16. "Clay" contents of soils (% by weight).

1	11	24	17	20	9	6	17	1	2
1	1	0	2	6	2	9	2	1	4
1	1	1	1	1	2	2	2	1	2
1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	0	1	1
0	1	0	1	1	1	1	1	1	1

+* 17. Dry weight (g.) of plants of P. lapathifolium per quadrat (1 m^2.).

35	6	167	59	41	42	114	72	97	54
4	111	15	14	16	25	12	14	11	4
3	-	1	3	14	-	1	5	17	35
-	43	19	14	2	-	-	-	-	-
-	-	18	24	4	-	21	-	-	13
4	9	0	-	-	10	7	3	-	-

Appendix II.6 (Continued)

+* 18. Dry weight (g.) of plants of P. pensylvanicum per quadrat (1 m^2.).

1	2	1	5	0	3	28	6	58	138
76	50	40	9	12	17	0	1	-	1
1	20	-	57	0	-	-	78	29	47
8	85	-	10	54	9	28	193	27	22
-	-	-	12	6	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-

+* 19. Dry weight (g.) of plants of P. persicaria per quadrat (1 m^2.).

-	-	-	-	4	-	-	-	-	-
2	2	-	-	-	-	-	-	-	-
-	1	-	-	-	-	-	-	-	-
-	12	4	-	7	-	-	-	-	-
-	-	-	5	-	-	-	-	-	-
-	-	-	-	-	4	-	-	-	-

Appendix II.7

Results of analyses used on the data in Survey IV, Chapter II to determine similarities and differences in dry weight of plants of a) P. lapathifolium between quadrat group and b) P. pensylvanicum between quadrat group.

a) P. lapathifolium

Results of analysis of variance of plant weights from 5 quadrat groups.

Source of variation	D.F.	S.S.	M.S.	F_s
Among groups	4	11171.9	2792.9	2.8266 *
Within groups (Error)	35	34583.1	988.0	
Total	39	45755.0		

$\chi^2_{0.05(4)} = 14.860$ (given) $\chi^2 = 13.582$

Results of Student - Newman - Keuls test for comparison of mean based on unequal sample sizes.

Quadrat group	B	C	E	A	D
Mean value for dry wt. (g.)	12.4	17.5	21.3	25.8	64.5

Values underscored by a common line are not significantly different from each other ($P > 0.05$)

Appendix II.7 (Continued)

b) P. pensylvanicum

Bartlett's test showed the variances to be significantly heterogeneous

$\chi^2 = 26.564$ ** given $\chi^2_{0.01(4)} = 13.277$, $\chi^2_{0.05(4)} = 14.860$

Results of an approximate F test which assumes that the variances are not homogeneous

Weighted Grand mean = 3.3816

Weighted correction term = 12.5477

Weighted sums of squares = 16.2543

F's for $v_1 = 4$ and $v_2 = 8$ df = 3.2514 *Given $F_{.05(4,8)} = 3.84$

This supports the hypothesis that the samples were drawn from populations with equal means, however, individual comparisons of means were made using an approximate t-test (Sokal and Rohlf 1969). The results are shown below.

Quadrat group	D	A	B	E	C
mean value for dry wt. (g.)	2.87	26.24	33.17	38.44	45.56
Values underscored by a common line were not significantly different from each other (P > 0.05)					

* significant (P < 0.05).

** significant (P < 0.01).

Appendix III.1 Analysis of categorical data.

Categorical data were obtained in many experiments described in this thesis. Information analysis was usually used to analyse this data. This test was found to be appropriate, easy to compute and has no "a priori" assumption that the data is normally distributed (Dr. L. Orloci, personal communication). Its application established values for total information and its components (i.e. factor effects, interaction effects, joint effect and experimental error). The following formulae gave the information content of each component for a R x C factorial model with one set of replicates for each factor component (Dr. L. Orloci, personal communication):

Variability in factor R,

$$2I = 2 \sum_{i=1}^{r} X_{i..} \ln \frac{X_{i..}/n_{i..}}{X_{...}/n_{...}}$$

Variability in factor C,

$$2I = 2 \sum_{j=1}^{c} X_{.j.} \ln \frac{X_{.j.}/n_{.j.}}{X_{...}/n_{...}}$$

Interaction of R and C,

$$2I = 2 \sum_{i=1}^{r} \sum_{j=1}^{c} X_{ij.} \ln \frac{X_{ij.}}{X_{i..}} \frac{X_{...}}{X_{.j.}} \frac{n_{i.}}{n_{ij}} \frac{n_{.j}}{n_{..}}$$

Joint information for R and C,

$$2\,I = 2 \sum_{i=1}^{r} \sum_{j=1}^{c} X_{ij.} \ln \frac{X_{ij.}/n_{ij}}{X_{...}/n_{..}}$$

Experimental error due to variation between the replicates within treatments,

$$2\,I = 2 \sum_{i=1}^{r} \sum_{j=1}^{c} \sum_{k=1}^{n_{ij}} X_{ijk} \ln \frac{X_{ijk}}{X_{ij.}/n_{ij}}$$

Total information based on individual variations from their common mean,

$$2\,I = 2 \sum_{i=1}^{r} \sum_{j=1}^{c} \sum_{k=1}^{n_{ij}} X_{ijk} \ln \frac{X_{ijk}}{X_{...}/n_{..}}$$

Comparisons between pairs of treatment means were then made (where meaningful). Such comparisons were only reliable if the expected value for each treatment mean was greater than 5 (Sokal and Rohlf 1969, pg. 565) and if the error term due to the differences between replicates within a treatment was not significant ($P > 5\%$). The information due to divergences of treatment means from their common mean is given by

$$2\,I = 2 \sum_{j=1}^{c} X_{j.} \ln \frac{X_{j.}/n_{j.}}{X_{..}/n_{..}}$$

The experimental error, due to variability between replicates, is given by

$$2I = 2 \sum_{j=1}^{c} \sum_{k=1}^{n_j.} X_{jk} \ln \frac{X_{jk}}{X_{j.}/n_{j.}}$$

Explanation of the symbols used in the above formulae:

2 I refers to information content. Factor R consists of c levels, each is arbitrarily given the symbol i. Factor C consists of r levels, each is given the symbol j. Each factor level has n_{ij} replicates, each of which is arbitrarily given the symbol k. Thus, the k th replicate of the j th level of factor C and the i th level of factor R has the value X_{ijk}. $X_{...}$ refers to the grand total of all replicates for all factor levels and factors. $X_{ij.}$ refers to the value of the replicate total for the i th level of R and the j th level of C. $X_{i..}$ refers to the value of the total of all values in the i th level in factor R and similarly, $X_{.j.}$ refers to the total of all values in the j th level in factor C. $n_{..}$ is the total number of samples $n_{..} = \Sigma \Sigma n_{ij}$, $n_{i.}$ is the number of samples in the i th level of R ($n_{i.} = \Sigma_{nij}$) and similarly, $n_{.j}$ is the number of samples in the j th level of C ($n_{.j} = \Sigma n_{ij}$).

Appendix III.2a. Table 1. Information analysis of the numbers of achenes floating in still water after 6 months. Comparisons of pairs of means were made and the results are shown in Table 2. (ns) not significant ($P > 0.5$). (**) significant ($P < 0.01$).

	D.F.	2 I	Significance
Main effect of species	2	4.594	ns
P. lap. - P. pens.	1	3.924	**
P. lap. - P. pers.	1	2.569	ns
P. pens. - P. pers.	1	0.020	ns
Main effect of achene condition	2	868.260	**
fresh - dry	1	20.547	**
fresh - o-winter	1	573.666	**
dry - o-winter	1	798.964	**
Main effect of perianth presence - absence	1	556.645	**
Interaction of factors	12	225.206	**
Experimental error	36	9.970	ns
Joint information	17	165.705	**
Total information	53	1664.675	**

Appendix III.2a. Table 2. Comparisons of pairs of means. No significant error terms were obtained in these combinations.

Between species

Achene condition	Perianth	Species pairs. P. lap/P. pens.	P. lap/P. pers.	P. pens./P. pers.
fresh	+	*	ns	ns
fresh	-	ns	*	ns
dry	+	ns	ns	ns
dry	-	**	**	ns
o-winter	+	ns	**	*
o-winter	-		data all zeros.	

Between achene conditions

Species	Perianth	Achene conditon pairs. fresh/dry	fresh/o-winter	dry/o-winter
P. lap.	+	**	**	**
P. lap.	-	**	**	**
P. pens.	+	ns	**	**
P. pens.	-	ns	**	**
P. pers.	+	ns	**	**
P. pers.	-	ns	**	**

continued...

Appendix III 2a. Table 2. (Continued)

Between perianth presence - absence

Species	Achene condition	Perianth present/absent
P. lap.	fresh	**
P. lap.	dry	**
P. lap.	o-winter	**
P. pens.	fresh	**
P. pens.	dry	**
P. pens.	o-winter	**
P. pers.	fresh	**
P. pers.	dry	**
P. pers.	o-winter	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 1. Information analysis of the numbers of achenes floating in agitated water after 0 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	40.486	**
P. lap. - P. pens.	1	35.770	**
P. lap. - P. pers.	1	22.452	**
P. pens. - P. pers.	1	1.380	ns
Main effect of achene condition	2	635.622	**
fresh - dry	1	37.282	**
fresh - o-winter	1	353.238	**
dry - o-winter	1	608.649	**
Main effect of perianth presence - absence	1	633.988	**
Interaction of factors	12	503.388	**
Experimental error	36	55.014	*
Joint information	17	1813.484	**
Total information	53	1868.498	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 2. Information analysis of the numbers of achenes floating in agitated water after 2 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	10.286	**
P. lap. - P. pens.	1	1.798	ns
P. lap. - P. pers.	1	10.179	**
P. pens. - P. pers.	1	3.246	ns
Main effect of achene condition	2	556.602	**
fresh - dry	1	9.308	**
fresh - o-winter	1	382.586	**
dry - o-winter	1	504.492	**
Main effect of perianth presence - absence	1	1497.343	**
Interaction of factors	12	153.618	**
Experimental error	36	36.684	ns
Joint information	17	2217.849	**
Total information	53	2254.533	**

ns not significant ($P > 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 3. Information analysis of the numbers of achenes floating in agitated water after 4 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	22.904	**
P. lap. - P. pens.	1	9.774	**
P. lap. - P. pers.	1	21.789	**
P. pens. - P. pers.	1	2.301	ns
Main effect of achene condition	2	561.710	**
fresh - dry	1	4.362	**
fresh - o-winter	1	415.419	**
dry - o-winter	1	498.799	**
Main effect of perianth presence - absence	1	(Values not analysed, too low)	
Interaction of factors	4	13.277	*
Experimental error	18	8.754	ns
Joint information	8	598.150	**
Total information	26	606.904	**

ns not significant ($P \geq 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 4. Information analysis of the numbers of achenes floating in agitated water after 8 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	43.726	**
P. lap. - P. pens.	1	25.554	**
P. lap. - P. pers.	1	37.362	**
P. pens. - P. pers.	1	1.082	ns
Main effect of achene condition	2	444.890	**
fresh - dry	1	4.976	*
fresh - o-winter	1	323.001	**
dry - o-winter	1	401.356	**
Main effect of perianth presence - absence	1	(Values not analysed, too low)	
Interaction of factors	4	28.066	**
Experimental error	18	27.088	ns
Joint information	8	516.683	**
Total information	26	543.771	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 5. Information analysis of the numbers of achenes floating in agitated water after 28 hours.

Component	D.F.	2·I	Significance
Main effect of species	2	41.230	**
P. lap. - P. pens.	1	21.208	**
P. lap. - P. pers.	1	6.635	**
P. pens. - P. pers.	1	2.120	ns
Main effect of achene condition	2	157.222	**
fresh - dry	1	1.935	ns
fresh - o-winter	1	113.686	**
dry - o-winter	1	142.581	**
Main effect of perianth presence - absence	1	(Values not analysed, too low)	
Interaction of factors	4	20.293	**
Experimental error	18	42.298	**
Joint information	8	218.748	**
Total information	26	261.046	**

ns not significant ($P > 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 6. Information analysis of the numbers of achenes floating in agitated water after 48 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	26.999	**
P. lap. - P. pens.	1	22.452	**
P. lap. - P. pers.	1	15.453	**
P. pens. - P. pers.	1	0.688	ns
Main effect of achene condition	2	98.935	**
fresh - dry	1	2.426	ns
fresh - o-winter	1	94.262	**
dry - o-winter	1	70.696	**
Main effect of perianth presence - absence	1	(Values not analysed, too low)	
Interaction of factors	4	7.540	ns
Experimental error	18	31.805	*
Joint information	8	134.549	**
Total information	26	166.354	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.2b. Table 7. Information analysis of the numbers of achenes floating in agitated water after 68 hours.

Component	D.F.	2 I	Significance
Main effect of species	2	15.476	**
P. lap. - P. pens.	1	15.395	**
P. lap. - P. pers.	1	1.998	ns
P. pens. - P. pers.	1	6.523	*
Main effect of achene condition	2	51.378	**
fresh - dry	1	5.143	*
fresh - o-winter	1	51.289	**
dry - o-winter	1	27.724	**
Main effect of perianth presence - absence	1	(Values not analysed, too low)	
Interaction of factors	4	9.850	*
Experimental error	18	17.864	ns
Joint information	8	76.704	**
Total information	26	94.568	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix III.3. 2I-values obtained by comparing the germination of agitated and non-agitated achenes. (ns) not significantly different at the 5% level, (*) significantly different at the 5% level, (**) significantly different at the 1% level.

Species	Achene condition	Perianth	Days after the start of germination test 5	10	20	30
P. lap.	fresh	+	48.52 **	35.43 *	28.91 **	23.40 **
P. lap.	fresh	-	3.29 ns	4.08 *	3.81 **	17.56 **
P. lap.	dry	+	144.78 **	16.04 *	2.78 ns	1.30 ns
P. lap.	dry	-	60.88 **	4.54 *	0.03 ns	0.04 ns
P. lap.	o-winter	+	18.40 **	8.92 **	7.37 **	6.08 *
P. lap.	o-winter	-	1.09 ns	3.70 **	3.53 ns	3.53 ns
P. pens.	fresh	+		Achenes dormant		
P. pens.	fresh	-		Achenes dormant		
P. pens.	dry	+		Achenes dormant		
P. pens.	dry	-		Achenes dormant		
P. pens.	o-winter	+	7.83 **	18.87 **	43.14 **	48.50 **
P. pens.	o-winter	-	2.84 ns	9.10 **	14.53 **	14.59 **
P. pers.	fresh	+		Achenes dormant		
P. pers.	fresh	-		Achenes dormant		
P. pers.	dry	+	2.91 ns	20.91 **	16.62 **	16.62 **
P. pers.	dry	-	10.97 **	31.50 **	23.64 **	20.89 **
P. pers.	o-winter	+	67.85 **	43.01 **	74.24 **	75.37 **
P. pers.	o-winter	-	30.89 **	43.31 **	36.33 **	26.27 **

Appendix IV.1.

Frequencies of species in 25 quadrats (1 m. x 1 m.) at the faeces collection site. (* refers to species which occurred in the faeces)

	Abutilon theophraste Medic.	1
	Acalypha rhomboidea Raf.	4
	Acer negundo L.	5
	Achillea millefolium L.	1
	Agropyron repens L.	1
*	Agrostis stolonifera L.	20
	Alliaria officinalis Andrz.	2
	Amaranthus retroflexus L.	1
	Ambrosia artemisiifolia L.	8
	Ambrosia trifida L.	3
	Arctium minus (Hill) Bernh.	5
	Asclepias incarnata L.	1
	Aster spp.	1
	Atriplex patula L.	1
*	Barbarea vulgaris R. Br.	16
	Bidens cernua L.	12
	Bidens frondosa L.	2
	Chaenorrhinum minus (L.) Lange	9
*	Chenopodium album L.	10
	Chenopodium glaucum L.	1
	Chrysanthemum leucanthemum L.	3
	Cirsium vulgare (L.) Scop.	2
	Cyperaceae spp. (vegetative)	9
	Cyperus esculentus L.	7
	Cyperus rivularis Kunth	5
	Dactylus glomerata L.	2
	Daucus carota L.	2
*	Digitaria ischaemum (Schreb.) Muhl.	1
	Digitaria sanguinalis (L.) Scop.	3
	Echinochloa crus-galli L.	21
	Echinocystis lobata (Minchx.) T. & G.	2
	Echium vulgare L.	1
	Eleocharis calva Torr.	8
	Eragrostis frankii Mey.	2
	Eragrostis pectinacea (Minchx.) Nees	11
	Erigeron annuus (L.) Beauv.	16
	Erigeron canadensis L.	2
	Erigeron philadelphicus L.	1
	Erysimum cheiranthoides L.	17
	Eupatorium maculatum L.	4
	Eupatorium perfoliatum L.	6
	Galium mollugo L.	7
	Galium palustre L.	2
	Glechoma hederacea L.	2
	Gnaphalium uliginosum L.	2

Appendix IV.1. (Continued)

	Hypericum perfoliatum L.	3
	Juncus articulatus L.	5
	Juncus dudleyi Wieg.	1
	Juncus nodosus L.	2
	Juncus tenuis Willd.	2
*	Leersia oryzoides L.	21
	Lemna minor L.	3
	Lepidium virginicum L.	1
	Linaria vulgaris Hill.	1
	Lychnis alba Mill.	1
	Lycopersicon esculentum Mill.	4
	Lycopus americanus Muhl.	1
*	Lythrum salicaria L.	20
	Medicago lupulina L.	17
	Medicago sativa L.	21
	Melilotus alba Desr.	1
	Mentha arvensis L.	1
	Mimulus ringens L.	5
*	Muhlenbergia frondosa (Poir.) Fern.	23
	Oenothera biennis L.	1
	Onopordum acanthium L.	1
	Panicum capillare L.	23
	Phalaris arundinacea L.	15
	Plantago lanceolata L.	4
*	Plantago major L.	23
*	Plantago rugelii Decne.	2
	Poa annua L.	1
	Poa compressa L.	1
	Polygonum aviculare L.	7
	Polygonum convolvulus L.	1
	Polygonum hydropiper L.	15
*	Polygonum lapathifolium L.	24
	Polygonum pensylvanicum L.	23
*	Polygonum persicaria L.	4
	Populus spp. (seedlings)	6
	Ranunculus repens L.	2
	Rorripa islandica (Oeder.) Borbas	2
	Rorripa sylvestris (L.) Bess.	1
	Rumex crispus L.	6
	Rumex obtusifolius L.	3
	Salix interior L.	10
	Salix rigida L.	7
	Saponaria officinalis L.	12
	Scutellaria galericulata L.	1
	Setaria viridis (L.) Beauv.	9
	Silene cucubalus Wibel	5
*	Solanum dulcamara L.	2
	Solanum nigrum L.	4
	Solidago spp. (vegetative)	7
	Stellaria aquatica (L.) Scop.	6
*	Stellaria media (L.) Cyrillo	14

Appendix IV.1. (Continued)

Trifolium hybridum L.	1
Trifolium pratense L.	1
Trifolium repens L.	9
Urtica dioica L.	1
Verbascum thapsus L.	2
Verbena hastata L.	13
Verbena urticifolia L.	15
Verbena spp. (vegetative plants)	19
Veronica serpyllifolia L.	3
Vitis riparia Michx.	1
Vitis vulpina L.	1
Xanthium strumarium L.	1
Zizia aurea (L.) W. D. J. Koch	1

Appendix IV.2. Excretion of fragmented and whole achenes by cottontails at intervals after the feeding period. Each mean is calculated from 3 replicates.

a) Whole achenes

Time after feeding.	Numbers of achenes excreted per hour			
	P. lapathifolium		P. persicaria	
	mean	S.E. of mean	mean	S.E. of mean
during feeding period	2.00	0.87	2.00	0.29
0 - 2 hrs.	1.33	0.17	0.50	0.29
2 - 4 hrs.	12.67	1.42	10.50	1.89
4 - 8 hrs.	9.25	1.01	8.08	1.42
8 - 12 hrs.	0.00	0.00	0.00	0.00
12 - 24 hrs.	1.31	0.10	1.30	0.10
24 - 48 hrs.	0.31	0.12	0.36	0.03
48 - 60 hrs.	0.00	0.00	0.00	0.00

b) Fragmented achenes

Time after feeding	Amounts of achenes excreted per hour (g.)			
	P. lapathifolium		P. persicaria	
	mean	S.E. of mean	mean	S.E. of mean
during feeding period	0.06	0.02	0.06	0.01
0 - 2 hrs.	0.01	0.005	0.01	0.003
2 - 4 hrs.	0.49	0.07	0.47	0.03
4 - 8 hrs.	0.29	0.07	0.27	0.07
8 - 12 hrs.	0.00	0.00	0.00	0.00
12 - 24 hrs.	0.03	0.01	0.03	0.01
24 - 48 hrs.	0.02	0.01	0.02	0.01
48 - 60 hrs.	0.00	0.00	0.00	0.00

Appendix IV.3.

a) Results of analysis of information on achene numbers (3 smartweed species) eaten by cottontails, data obtained in experiment 3, chapter IV.

Source of information	D.F.	Information
Main effects		
Species	2	1.34 n.s.
P. lapathifolium - P. pensylvanicum	1	0.71 n.s.
P. lapathifolium - P. persicaria	1	0.27 n.s.
P. pensylvanicum - P. persicaria	1	0.90 n.s.
Error	9	8.87 n.s.
Total	11	10.21 n.s.

b) Results of analysis of information on numbers of viable achenes (2 smartweed species) after excretion by cottontails, data obtained in experiment 3, chapter IV.

Source of information	D.F.	Information
Main effect		
Species		
P. lapathifolium - P. persicaria	1	13.53 **
Error	6	4.20 n.s.
Total	7	17.73 *

n.s. not significant at 5% level

* significant at 5% level

** significant at 1% level

Appendix IV.4.

Results of analyses of variance on the lengths and widths of achenes in 9 species/achene size combinations, data from experiment 4, chapter IV. For both achene lengths and achene widths means were compared between pairs of species/achene size combinations using the Student-Newman-Keuls Test (Sokal and Rohlf 1969, pg. 239).

a) Achene lengths.

Source of s.s.	D.F.	S.S.	M.S.	F.S.
Main effect Species/achene lengths	8	11187.24	1398.40	675.75***
Error	441	912.59	2.07	
Total	449	12099.83		

b) Achene widths.

Source of s.s.	D.F.	S.S.	M.S.	F.S.
Main effect Species/achene widths	8	17036.97	2129.62	1237.65***
Error	441	758.83	1.72	
Total	449	17795.80		

*** significant at the 0.1% level.

Appendix IV.5

a) A summary of analysis of information on the numbers of achenes eaten by cottontails, using 3 species of smartweeds and 3 achene size categories. Data from experiment 4, Chapter IV.

Source of Information	D.F.	Information
Main effects		
Effect of species	2	5.8032 ns
Effect of achene size categories	2	4.3972 ns
Interaction	4	0.2040 ns
Joint effect	8	10.4044 ns
Error	18	21.7352 ns
Total	26	32.1396 ns

ns , no significant difference at the 5% level

Appendix IV.5 (Continued)

b) Pairwise comparisons were made of numbers of eaten achenes between species and achene size categories. Treatments underscored by a common line show no significant difference at the 5% level. Significant heterogeneity at the 5% level was found between the replicates and the means of each pair of treatments associated with the same letter.

Smallest number eaten → largest number eaten

P. lap.[ab] l	P. lap. s	P. pers.[a] l	P. pers. a	P. lap.[b] m	P. pens. s	P. pens. l	P. pens, m	P. pers. m

P. lap. = P. lapathifolium
P. pens. = P. pensylvanicum
P. pers. = P. persicaria

s small achene category
m medium achene category
l large achene category

Appendix IV.6.

a) Results of analysis of information on the numbers of viable achenes excreted by cottontails, data from experiment 4, Chapter IV. Consideration is given to 2 species of smartweeds (no viable achenes occurred for P. pensylvanicum) and 3 achene size categories.

Source of Information	D.F.	Information
Main effects		
Effect of species	1	51.737 **
Effect of acheny size categories	2	64.332 **
small - medium	1	50.058 **
small - large	1	47.855 **
medium - large	1	24.448 **
Interaction	2	54.600 **
Joint effect	5	170.669 **
Error	12	7.157 ns
Total	17	177.826 **

ns not significant at the 5% level

** significant at the 1% level

b) Pairwise comparisons were made of the numbers of viable achenes between species and achene size categories. Treatments underscored by a common line show no significant difference at the 5% level.

lowest viability					highest viability
P. pers. l	P. lap. l	P. pers. m	P. lap. m	P. pers. s	P. lap. s

P. lap. P. lapathifolium

P. pers. P. persicaria

s small achene category

m medium achene category

l large achene category

No significant heterogeneity at the 5% level was found between the replicates and the means of each pair of treatments.

Appendix V.1. Results of information analysis on germination data from the preliminary germination tests (not tested at P = 0.001 level).

Source of information	DF	Information	Probability
Main effect of spp.	2	441.835	**
lap. & pens.	1	421.257	**
lap. & pers.	1	165.240	**
pens. & pers.	1	65.083	**
Main effect of germ. temps.	2	739.084	**
effect of temps. 1&2	1	91.463	**
effect of temps. 1&3	1	644.909	**
effect of temps. 2&3	1	306.364	**
Interaction	4	7.992	ns
Joint effect	8	1188.911	**
Experimental Error	27	34.790	ns
Total Information	35	1223.701	**

Appendix V.1. (Continued)

Individual comparisons.

Between temperatures within species.

a) P. persicaria

Source of information	DF	Information	Probability
Main effect of germ. temp.	2	156.708	**
temps. 1&2	1	28.140	**
temps. 1&3	1	143.294	**
temps. 2&3	1	55.883	**
Experimental Error	9	14.035	ns
Total information	11	170.743	**

b) P. lapathifolium

Source of information	DF	Information	Probability
Main effect of temps.	2	559.930	**
temps. 1&2	1	52.700	**
temps. 1&3	1	471.810	**
temps. 2&3	1	253.656	**
Experimental Error	9	22.644	**

Appendix V.1. (Continued)

c) P. pensylvanicum

Source of information	DF	Information	Probability
Main effect of temps.	2	30.092	**
temps. 1&2	1	---	--
temps. 1&3	1	---	--
temps. 2&3	1	5.918	**
Experimental Error	9	5.750	ns
Total information	11	36.142	**

Between species differences.

a) Temperature 1.

Source of information	DF	Information	Probability
Main effect of spp.	2	5.934	ns
pers. & lap.	1	2.940	ns
lap. & pens.	1	---	--
pers. & pens.	1	---	--
Experimental Error	9	8.802	ns
Total information	11	14.736	ns

Appendix V.1. (Continued)

b) Temperature 2.

Source of Information	DF	Information	Probability
Main effect of spp.	2	40.654	**
pers. & lap.	1	13.495	**
pers. & pen.	1	7.264	**
lap. & pen.	1	39.055	**
Experimental Error	9	18.218	
Total information	11	58.872	**

c) Temperature 3.

Source of Information	DF	Information	Probability
Main effect of spp.	2	403.196	**
pers. & lap.	1	151.418	**
pers. & pen.	1	59.661	**
lap. & pen.	1	510.640	**
Experimental Error	9	9.740	ns
Total information	11	412.936	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

--- no comparison made

Appendix V.2. Results of information analyses on germination data concerning achenes stored in two storage sites for seven durations.

Source of Information	DF	Information	Probability
Main effect of species	2	1043.458	**
spp. 1 & 2	1	405.586	**
spp. 1 & 3	1	996.968	**
spp. 2 & 3	1	132.518	**
Main effect of retrieval dates	6	2214.871	**
Dates 4 & 5 (closest)	1	20.991	**
Main effect of storage site	1	73.406	**
Interaction (spp., date, site)	12	1407.924	**
Joint Information	41	4739.659	**
Experimental Error	126	40.500	ns
Total	167	4780.159	**

Appendix V.2. (Continued) Experiment 2, species comparisons.

Site a) outdoors.

	Source of Information	DF	Information	Probability
Time 1.	Main effect of spp.	2	318.077	**
	spp. 1 & 2	1	215.285	**
	spp. 1 & 3	1	200.971	**
	spp. 2 & 3	1	0.476	ns
	Error	9	7.907	ns
	Total	11	325.984	**
Time 2.	Main effect of spp.	2	416.615	**
	spp. 1 & 2	1	232.128	**
	spp. 1 & 3	1	226.747	**
	spp. 2 & 3	1	10.753	**
	Error	9	2.646	ns
	Total	11	419.261	**
Time 3.	Main effect of spp.	2	265.565	**
	spp. 1 & 2	1	83.500	**
	spp. 1 & 3	1	256.447	**
	spp. 2 & 3	1	52.248	**
	Error	9	5.446	ns
	Total	11	271.011	**

Appendix V.2. (Continued) Experiment 2, species comparisons continued.

	Source of Information	DF	Information	Probability
Time 4.	Main effect of spp.	2	83.211	**
	spp. 1 & 2	1	15.960	**
	spp. 1 & 3	1	83.160	**
	spp. 2 & 3	1	26.616	**
	Error	9	10.429	ns
	Total	11	93.640	**
Time 5.	Main effect of spp.	2	58.616	**
	spp. 1 & 2	1	3.531	ns
	spp. 1 & 3	1	55.357	**
	spp. 2 & 3	1	30.891	**
	Error	9	2.350	ns
	Total	11	60.966	**
Time 6.	Main effect of spp.	2	35.509	**
	spp. 1 & 2	1	3.153	ns
	spp. 1 & 3	1	34.226	**
	spp. 2 & 3	1	16.504	**
	Error	9	4.194	ns
	Total	11	39.703	**

Appendix V.2. (Continued) Experiment 2, species comparisons - continued.

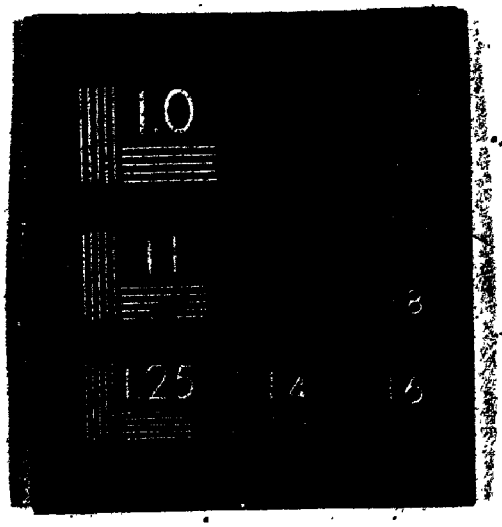
Time 7.	Source of Information	DF	Information	Probability
	Main effect of spp.	2	0.115	ns
	spp. 1 & 2	1	0.069	ns
	spp. 1 & 3	1	0.053	ns
	spp. 2 & 3	1	0.008	ns
	Error	9	0.355	ns
	Total	11	0.470	ns

Site b) inside.

Time 1.	Main effect of spp.	2	331.830	**
	spp. 1 & 2	1	233.987	**
	spp. 1 & 3	1	197.131	**
	spp. 2 & 3	1	3.381	ns
	Error	9	3.182	ns
	Total	11	335.012	**
Time 2.	Main effect of spp.	2	208.065	**
	spp. 1 & 2	1	136.757	**
	spp. 1 & 3	1	145.118	**
	spp. 2 & 3	1	0.161	ns
	Error	9	5.043	ns
	Total	11	213.138	**

5 5

OF/DE



Appendix V.2. (Continued) Experiment 2, species comparisons - continued.

	Source of Information	DF	Information	Probability
Time 3.	Main effects of spp.	2	224.335	**
	spp. 1 & 2	1	93.162	**
	spp. 1 & 3	1	204.226	**
	spp. 2 & 3	1	24.705	**
	Error	9	2.659	ns
	Total	11	226.994	**
Time 4.	Main effect of spp.	2	106.318	**
	spp. 1 & 2	1	43.782	**
	spp. 1 & 3	1	106.822	**
	spp. 2 & 3	1	14.480	**
	Error	9	6.412	ns
	Total	11	112.730	**
Time 5.	Main effect of spp.	2	67.098	**
	spp. 1 & 2	1	33.235	**
	spp. 1 & 3	1	60.600	**
	spp. 2 & 3	1	4.139	*
	Error	9	1.633	ns
	Total	11	68.731	**

Appendix V.2. (Continued) Experiment 2, species comparisons - continued.

	Source of Information	DF	Information	Probability
Time 6.	Main effect of spp.	2	65.636	**
	spp. 1 & 2	1	0.213	ns
	spp. 1 & 3	1	54.342	**
	spp. 2 & 3	1	46.805	**
	Error	9	1.025	ns
	Total	11	66.661	**
Time 7.	Main effect of spp.	2	0.072	ns
	spp. 1 & 2	1	---	ns
	spp. 1 & 3	1	---	ns
	spp. 2 & 3	1	---	ns
	Error	9	0.1106	ns
	Total	11	0.1826	ns

spp. 1 *P. lapathifolium*

spp. 2 *P. pensylvanicum*

spp. 3 *P. persicaria*

ns not significant ($P > 0.05$)

* significant ($P < 0.05$).

** significant ($P < 0.01$).

--- no comparison made

Appendix V.3. (see Experiment 3, Chapter V). Results of information analysis of achenes of three species of Polygonum stored for four durations in thirteen storage conditions.

Source of Information	DF	Information	Probability
Species	2	2968.169	**
P. lap./P. pens.	1	1770.346	**
P. lap./P. pens.	1	2446.729	**
P. pens./P. pers.	1	61.793	**
Withdrawal times	3	1210.476	**
Feb./Mar.	1	139.318	**
Feb./May	1	167.137	**
Feb./Aug.	1	1192.643	**
Mar./May	1	6.270	*
Mar./Aug.	1	468.941	**
May/Aug.	1	495.422	**
Storage conditions	12	13363.335	**
a/b/c/d/e	4	864.105	**
f/g/h/i	3	1615.652	**
j/k/l/m	3	909.803	**
e/f/j	2	1042.242	**
i/m	1	4051.981	**
a/g/k	2	1958.048	**
a/h/l	2	3971.123	**
Interaction	72	9360.560	**
Joint Information	155	26902.540	**
Experimental Error	468	221.482	ns
Total Information	623	27124.022	**

Appendix V.3. (Continued) Results of information analysis on data for germination under laboratory conditions of achenes of P. lapathifolium stored for four durations in thirteen storage conditions.

Source of Information	DF	Information	Probability
Withdrawal times	3	70.613	**
Feb./Mar.	1	3.795	ns
Feb./May	1	0.060	ns
Feb./Aug.	1	54.940	**
Mar./May	1	7.207	**
Mar./Aug.	1	28.316	**
May/Aug.	1	65.878	**
Storage conditions	12	5816.458	**
a/b/c/d/e	4	164.832	**
f/g/h/i	3	1157.780	**
j/k/l/m	3	80.671	**
e/f/j	2	270.342	**
a/h/l	2	1783.770	**
i/m	1	1932.274	**
a/g/k	2	1517.103	**
Interaction	36	992.400	**
Joint Information	51	6879.471	**
Experimental Error	156	69.123	ns
Total Information	207	6948.594	**

Appendix V.3 (Continued) Results of information analysis on data for laboratory germination of achenes of P. pensylvanicum stored for four durations in thirteen storage conditions.

Source of Information	DF	Information	Probability
Withdrawal times	3	783.608	**
Feb./Mar.	1	1.290	ns
Feb./May	1	0.731	ns
Feb./Aug.	1	598.802	**
Mar./May	1	0.258	ns
Mar./Aug.	1	539.933	**
May/Aug.	1	550.942	**
Storage conditions	12	7066.706	**
a/b/c/d/e	4	595.595	**
f/g/h/i	3	25.865	**
j/k/l/m	3	2609.037	**
e/f/j	2	977.314	**
a/h/l	2	1641.688	**
i/m	1	1601.545	**
a/g/h	2	490.816	**
Interaction	36	1961.892	**
Joint Information	51	9812.361	**
Experimental Error	156	56.051	ns
Total Information	207	9868.412	**

Appendix V.3. (Continued) Results of information analysis on data for laboratory germination of achenes of P. persicaria stored for four durations in thirteen storage conditions.

Source of Information	DF	Information	Probability
Withdrawal times	3	1404.405	**
Feb./Mar.	1	386.924	**
Feb./May	1	671.851	**
Feb./Aug.	1	1234.754	**
Mar./May	1	40.666	**
Mar./Aug.	1	256.400	**
May/Aug.	1	93.946	**
Storage conditions	12	3796.261	**
a/b/c/d/e	4	489.018	**
f/g/h/i	3	478.129	**
j/k/l/m	3	567.556	**
e/f/j	2	435.225	**
a/h/l	2	701.690	**
i/m	1	522.507	**
a/g/k	2	327.248	**
Interaction	36	2051.872	**
Joint Information	51	7252.538	**
Experimental Error	156	96.308	ns
Total Information	207	7348.846	**

Appendix V.3. (Continued). Results of information analysis on percentage germination in the field after 11 months for achenes of three species of Polygonum and thirteen sites.

Source of Information	DF	Information	Probability
Species	2	51.200	**
P. lap./P. pens.	1	46.499	**
P. lap./P. pers.	1	25.106	**
P. pens./P. pers.	1	3.305	ns
Sites	12	1080.009	**
a/b/c/d/e	4	693.759	**
f/g/h/i	3	152.816	**
j/k/l/m	3	78.875	**
e/f/j	2	NO GERMINATION	
i/m	1	14.720	**
a/g/k	2	68.496	**
a/h/l	2	50.818	**
Interaction	24	581.400	**
Joint Information	38	1712.609	**
Experimental Error	117	32.891	ns
Total Information	155	1745.500	**

Appendix V.3. (Continued) Results of information analysis on percentages of achenes dormant in the field after 11 months storage for three species and thirteen sites.

Source of Information	DF	Information	Probability
Species	2	1449.874	**
P. lap./P. pens.	1	13.975	**
P. lap./P. pers.	1	1004.355	**
P. pens./P. pers.	1	1257.156	**
Sites	12	493.786	**
a/b/c/d/e	4	254.741	**
f/g/h/i	3	81.161	**
j/k/l/m	3	71.246	**
e/f/j	2	28.131	**
a/h/l	2	37.826	**
i/m	1	2.437	ns
a/g/k	2	37.589	**
Interaction	24	1568.430	**
Joint Information	38	3512.090	**
Experimental Error	117	39.182	ns
Total Information	155	3551.272	**

Appendix V.3. (Continued) Results of information analysis on percentages of achenes inviable in the field after 11 months storage for three species and thirteen sites.

Source of Information	DF	Information	Probability
Species	2	2538.719	**
P. lap./P. pens.	1	32.837	**
P. lap./P. pers.	1	1526.603	**
P. pens./P. pers.	1	1970.414	**
Storage conditions	12	590.002	**
a/b/c/d/e	4	104.422	**
f/g/h/i	3	221.400	**
j/k/l/m	3	183.426	**
e/f/j	2	96.333	**
a/h/l	2	142.737	**
i/m	1	2.260	ns
a/g/k	2	104.234	**
Interaction	24	451.174	**
Joint Information	38	3579.895	**
Experimental Error	117	79.489	ns
Total Information	155	3659.384	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix V.4. (see Experiment 4, Chapter V) Results of information analysis on data for total germination of achenes of 3 species of Polygonum stored at two depths in agricultural soil and retrieved at three times during the year (3 factorial analysis).

Source of Information	DF	Information	Probability
Species	2	17.620	**
P. lap./P. pens.	1	16.764	**
P. lap./P. pers.	1	7.237	**
P. pens./P. pers.	1	1.664	ns
Time of sowing	2	13.122	**
Spring/summer	1	0.549	ns
Spring/autumn	1	12.069	**
Summer/autumn	1	6.499	**
Depth of burial (6/60 cm.)	1	2.126	ns
Interaction	4	12.792	*
Joint Information	17	45.660	**
Experimental Error	36	11.532	ns
Total Information	53	57.192	ns

Appendix V.4. (Continued) Information analysis on germination from spring sowing of achenes previously stored at the soil surface (1-factorial analysis).

Source of Information	DF	Information	Probability
Species	2	14.421	**
P. lap./P. pens.	1	10.083	**
P. lap./P. pers.	1	11.090	**
P. pens./P. pers.	1	0.011	ns
Experimental Error	6	1.833	ns
Total Information	8	16.254	*

Appendix V.4. (Continued) Results of information analysis on percentage germination data for achenes stored at two soil depths and retrieved after three time periods (sowing times). (2-factorial analysis)

Source of Information	DF	Information	Probability
a) P. lapathifolium			
Sowing time	2	6.022	*
spring/summer	1	0.836	ns
spring/autumn	1	5.891	*
summer/autumn	1	2.090	ns
Soil depth	1	0.083	ns
Experimental Error	12	1.710	ns
Total Information	18	13.606	ns
b) P. pensylvanicum			
Sowing time	2	5.307	ns
spring/summer	1	0.080	ns
spring/autumn	1	3.750	ns
summer/autumn	1	4.142	*
Soil depth	1	1.244	ns
Experimental Error	12	5.477	ns
Total Information	18	12.376	ns
c) P. persicaria			
Sowing time	2	2.744	ns
spring/summer	1	0.359	ns
spring/autumn	1	2.665	ns
summer/autumn	1	0.887	ns
Soil depth	1	3.510	ns
Experimental Error	12	4.344	ns
Total Information	18	14.306	ns

Appendix V.4. (Continued) Results of information analysis on percentage germination data for achenes of three species of Polygonum stored at two soil depths. (2-factorial analysis)

Source of Information	DF	Information	Probability
a) Spring sowing			
Species	2	8.376	*
P. lap./P. pens.	1	8.318	**
P. lap./P. pers.	1	3.650	ns
P. pens./P. pers.	1	0.841	ns
Soil storage depth	1	1.427	ns
Experimental Error	12	2.904	ns
Total Information	18	13.848	ns
b) Summer sowing			
Species	2	4.048	ns
P. lap./P. pens.	1	3.272	ns
P. lap./P. pers.	1	2.593	ns
P. pens./P. pers.	1	0.052	ns
Soil storage depth	1	0.689	ns
Experimental Error	12	5.186	ns
Total Information	18	10.556	ns
c) Autumn sowing			
Species	2	5.787	ns
P. lap./P. pens.	1	5.732	*
P. lap./P. pers.	1	1.232	ns
P. pens./P. pers.	1	1.517	ns
Soil storage depth	1	0.204	ns
Experimental Error	12	3.441	ns
Total Information	18	20.380	ns

Appendix V.4. (Continued) Results of information analyses on percentage germination data for achenes of three species of Polygonum removed from storage site and sown at three times. (2-factorial analysis)

Source of Information	DF	Information	Probability
a) Stored at 6 cm.			
Species	2	15.259	**
P. lap./P. pens.	1	13.073	**
P. lap./P. pers.	1	9.051	**
P. pens./P. pers.	1	0.240	ns
Sowing times	2	4.984	ns
spring/summer	1	0.840	ns
spring/autumn	1	4.450	*
summer/autumn	1	2.656	ns
Experimental Error	18	4.107	ns
Total Information	26	27.828	ns
b) Stored at 60 cm.			
Species	2	4.905	ns
P. lap./P. pens.	1	4.753	*
P. lap./P. pers.	1	0.614	ns
P. pens./P. pers.	1	1.667	ns
Sowing times	2	8.331	*
spring/summer	1	0.517	ns
spring/autumn	1	7.184	**
summer/autumn	1	3.887	*
Experimental Error	18	7.424	ns
Total Information	26	26.647	ns

Appendix V.4. (Continued) Results of information analysis on percentage germination data, comparing the sizes of the first flushes of germination for each species, soil storage depth and sowing date. (3-factorial analysis)

Source of Information	DF	Information	Probability
Species	2	228.398	**
P. lap./P. pens.	1	228.002	**
P. lap./P. pers.	1	41.209	**
P. pens./P. pers.	1	76.067	**
Sowing dates	2	22.846	**
spring/summer	1	3.689	ns
spring/autumn	1	22.429	**
summer/autumn	1	7.628	**
Soil storage depth 6 cm./60 cm.	1	0.120	ns
Interaction	4	111.820	**
Joint Information	17	363.184	**
Experimental Error	36	21.970	**
Total Information	53	385.154	**

Appendix V.4. (Continued) Results of information analysis on percentage germination data, comparing the sizes of the second flushes, for each species, soil storage depth and sowing date.

Source of Information	DF	Information	Probability
Species	2	46.903	**
P. lap./P. pens.	1	43.301	**
P. lap./P. pers.	1	3.572	ns
P. pens./P. pers.	1	22.041	**
Sowing dates	2	21.710	**
spring/summer	1	0.076	ns
spring/autumn	1	16.222	**
summer/autumn	1	16.770	**
Soil depth 6 cm./60 cm.	1	10.017	**
Interaction	4	184.420	**
Joint Information	17	263.050	**
Experimental Error	36	42.870	ns
Total Information	53	305.920	**

Appendix V.4. (Continued) Results of information analysis on percentage germination data, comparing the sizes of the third flushes, for each species, soil storage depth and sowing date.

Source of Information	DF	Information	Probability
Species	2	189.884	**
P. lap./P. pens.	1	188.940	**
P. lap./P. pers.	1	59.208	**
P. pens./P. pers.	1	40.634	**
Sowing dates			
spring/summer	1	41.973	**
Soil storage depth 6 cm./60 cm.	1	1.667	ns
Interaction	2	164.090	**
Joint Information	11	397.614	**
Experimental Error	24	21.344	ns
Total Information	35	418.958	**

Appendix V.4. (Continued) Results of information analysis on percentage germination flush for achenes of each species and from each storage depth. (3-factorial analysis)

a) Spring sowing

Source of Information	DF	Information	Probability
Species	2	8.736	*
P. lap./P. pens.	1	8.318	**
P. lap./P. pers.	1	3.650	ns
P. pens./P. pers.	1	0.841	ns
Germination flushes	2	287.088	**
1st/2nd flush	1	115.663	**
1st/3rd flush	1	270.446	**
2nd/3rd flush	1	33.803	**
Soil storage depth 6 cm./60 cm.	1	1.427	ns
Interaction	4	284.238	**
Joint Information	17	581.489	**
Experimental Error	36	32.708	ns
Total Information	53	614.197	**

Appendix V.4. (Continued) Results of information analysis on percentage germination data, comparing the sizes of each germination flush for achenes of each species and from each storage depth. (3-factorial analysis)

b) Summer sowing

Source of Information	DF	Information	Probability
Species	2	4.048	ns
P. lap./P. pens.	1	3.272	ns
P. lap./P. pers.	1	2.593	ns
P. pens./P. pers.	1	0.052	ns
Germination flushes	2	603.728	**
1st/2nd flush	1	159.434	**
1st/3rd flush	1	594.148	**
2nd/3rd flush	1	150.437	**
Soil storage depth 6 cm./60 cm.	1	0.689	ns
Interaction	4	387.062	**
Joint Information	17	995.527	**
Experimental Error	36	34.284	ns
Total Information	53	1029.811	**

Appendix V.4. (Continued) Results of information analysis on percentage germination data, comparing the sizes of each germination flush for achenes of each species and from each storage depth. (3-factorial analysis)

c) Autumn sowing

Source of Information	DF	Information	Probability
Species	2	5.787	ns
P. lap./P. pens.	1	5.732	*
P. lap./P. pers.	1	1.231	ns
P. pens./P. pers.	1	1.517	ns
Germination flushes			
1st/2nd flush (no 3rd flush)	1	374.274	**
Soil storage depth 6 cm./60 cm.	1	0.204	ns
Interaction	2	243.688	**
Joint Information	11	623.953	**
Experimental Error	24	19.091	ns
Total Information	35	643.044	**

ns not significant ($P > 0.05$)

* significant ($P < 0.05$)

** significant ($P < 0.01$)

Appendix VI.1.

a) A summary of analysis of information on the numbers of pregerminated achenes emerged from soils with different water contents, using three species of smartweeds. Data from Experiment 1, Chapter VI.

Source of Information	DF	Information
Main effects		
Effect of soil water content	5	160.764 **
soil water contents (a) and (b)	1	18.021 **
soil water contents (b) and (c)	1	31.804 **
soil water contents (c) and (d)	1	0.769 ns
soil water contents (c) and (e)	1	0.928 ns
soil water contents (c) and (f)	1	1.098 ns
Effect of species	2	0.270 ns
Interaction	10	2.036 ns
Joint Information	17	163.070 **

Experimental Error and Total Information not calculated as data consists of one replicate per treatment.

For Key to abbreviations used above see next page.

Appendix VI.1. (Continued)

b) Pairwise comparisons were made on the numbers of pregerminated achenes to emerge within species and soil water content values using information analysis. Values associated with the same letter are not significantly different (P = 0.05).

	Emergence (24 planted)		
	P. lap.	R. pens.	P. pers.
Soil water content			
(a)	0	0	0
(b)	3^{y}	4^{y}	6^{y}
(c)	17^{x}	19^{x}	23^{x}
(d)	24^{x}	24^{x}	21^{x}
(e)	23^{x}	24^{x}	23^{x}
(f)	23^{x}	24^{x}	24^{x}

Low values cannot be compared accurately with other values unless their mean equals or is greater than 2 (Snedecor and Cochran 1967). Hence 0 and 3 cannot be compared, whereas 0,4 can (not significantly different P = 0.05). 0 can be compared with all other values above 4 (significantly different, P = 0.05).

Appendix VI.1. (Continued)

Key to abbreviations used on the preceding two pages.

ns	no significant difference at the 5% level
**	significantly different at the 1% level
P. lap.	Polygonum lapathifolium
P. pens.	P. pensylvanicum
P. pers.	P. persicaria

Soil water contents:

(a)	soil level 4.5 cm. below water level
(b)	soil level equal to water level
(c)	soil level 4.5 cm. above water level
(d)	soil level 10.0 cm. above water level
(e)	soil level 18.0 cm. above water level
(f)	soil watered from above only
SNK	Student-Newman-Keuls test

Appendix VI.2 Results of Bartlett's tests on raw and transformed data obtained in Experiment 1, Chapter VI, and subsequent choice of statistical tests.

	Bartlett's test - adjusted χ^2				
	$\chi^2_{.05(11)}$	Raw data	$\sqrt{\text{trans.}}$	log. trans.	subsequent analysis
1. Dry weight	19.675	618.684*	228.669*	62.578*	STP
2. Root dry weight/ total dry weight	19.675	376.283*	95.452*	108.925*	STP
3. Shoot length	19.675	200.133*	70.177*	113.971*	STP
4. Root length	19.675	95.442*		2.941^{ns}	2-way anova on log. data

* significantly heterogeneous variances ($P < 0.05$)

ns variances not significantly heterogeneous ($P > 0.05$)

STP Simultaneous test procedure

Appendix VI.3. Results of STP analysis (Sokal and Rohlf 1969) on dry weights of plants of three species of Polygonum grown under four soil water contents, giving the calculated and estimated values of U. See Experiment 1, Chapter VI and Figure VI.2.

a) Between species comparisons

Soil water contents	Pairwise comparisons Calculated U-values			Estimated U-value
	P. lap. -P. pens.	P. lap. -P. pers.	P. pens. -P. pers.	
(c)	571.5*	564.5*	357.0 ns	401.6
(d)	514.5*	576.0*	576.0*	401.6
(e)	576.0*	460.5*	576.0*	401.6
(f)	576.0*	402.0*	570.5*	401.6

b) Between soil water contents comparisons

Species	Pairwise comparisons Calculated U-values						Estimated U-value
	c-d	c-e	c-f	d-e	d-f	e-f	
P. lap.	576.0*	576.0*	568.5*	329.5^{ns}	576.0*	576.0*	412.6
P. pens.	576.0*	576.0*	576.0*	410.0^{ns}	565.0*	576.0*	412.6
P. pers.	518.5*	576.0*	566.5*	576.0*	522.0*	575.5*	412.6

Values for soil water contents (a) and (b) were not used owing to poor seedling emergence.

Key to abbreviations and symbols on the following page.

Appendix VI.3 (Continued)

Key to abbreviations and symbols

STP	Simultaneous test procedure
ns	values not significantly different ($P > 0.05$)
*	values significantly different ($P < 0.05$)
P. lap.	Polygonum lapathifolium
P. pens.	P. pensylvanicum
P. pers.	P. persicaria

Soil water contents:

(a)	soil level 4.5 cm. below water level
(b)	soil level equal to water level
(c)	soil level 4.5 cm. above water level
(d)	soil level 10.0 cm. above water level
(e)	soil level 18.0 cm. above water level.
(f)	soil watered from above only

Appendix VI.4 Results of STP analysis (Sokal and Rohlf 1969) on shoot lengths of plants of three species of Polygonum grown under four soil water contents, giving the calculated and estimated values of U. See Experiment 1, Chapter VI and Figure VI.3.

a) Between species comparisons

Soil water contents	Pairwise comparisons Calculated U-values			Estimated U-value
	P. lap. -P. pens.	P. lap. -P. pers.	P. pens. -P. pers.	
(c)	497.5*	434.0*	387.5 ns	401.6
(d)	377.5 ns	541.5*	512.0*	401.6
(e)	555.0*	516.5*	576.0*	401.6
(f)	536.5*	391.5 ns	563.[illegible]	401.6

b) Between soil water contents comparisons

Species	Pairwise comparisons Calculated U-values						Estimated U-value
	c-d	c-e	c-f	d-e	d-f	e-f	
P. lap.	576.0*	576.0*	576.0*	506.0*	569.5*	549.5*	412.6
P. pens.	576.0*	576.0*	576.0*	313.0^{ns}	460.0*	547.0*	412.6
P. pers.	576.0*	[illegible]*	555.5*	334.0^{ns}	505.0*	434.0*	412.6

Values for soil water contents (a) and (b) were not used owing to poor seedling emergence.

For key to abbreviations and symbols see Appendix VI.3.

Appendix VI.5. Results of STP analysis (Sokal and Rohlf 1969) on root weight as a percentage of total dry weight for plants of three species of Polygonum, grown under four soil water contents, giving the calculated and estimated values of U. See Experiment 1, Chapter VI and Table VI.3.

a) Between species comparisons

Soil water contents	Pairwise comparisons Calculated U-values			Estimated U-value
	P. lap. -P. pens.	P. lap. -P. pers.	P. pens. -P. pers.	
(c)	429.5*	498.5*	354.5 ns	401.6
(d)	294.0 ns	576.0*	576.0*	401.6
(e)	468.5*	481.5*	293.0 ns	401.6
(f)	302.0 ns	526.0*	533.0*	401.6

b) Between soil water contents comparisons

Species	Pairwise comparisons Calculated U-values						Estimated U-value
	c-d	c-e	c-f	d-e	d-f	e-f	
P. lap.	576.0*	576.0*	576.0*	516.5*	465.5*	515.0*	412.6
P. pens.	576.0*	571.0*	538.5*	366.5 ns	473.5*	484.0*	412.6
P. pers.	558.0*	576.0*	576.0*	576.0*	576.0**	460.0*	412.6

Values for soil water contents (a) and (b) were not used owing to poor seedling emergence.

Key to abbreviations and symbols in Appendix VI.3.

Appendix VI.6.

a) Results of two-way analysis of variance on root lengths (log. transformed data) of plants of three species of Polygonum grown under four soil water contents. See Experiment 1, Chapter VI and Figure VI.4.

Source of variation	D.F.	S.S.	M.S.	F.
Subgroups	11	3.0931	0.2812	
A (soil water contents)	3	1.7731	0.3591	18.3214 ***
B (species)	2	0.1648	0.0824	4.2041 *
AxB (interaction)	6	1.1552	0.1925	9.8214 ***
Within groups	276	5.4125	0.0196	
Total	287	8.5056		

for log. transformed data = 2.941^{ns}

ns not significant ($P > 0.05$)

* significantly different ($P < 0.05$)

*** significantly different ($P < 0.001$)

Appendix VI.6. (Continued)

b) Results of pairwise comparisons of root lengths (log. cm.) using the SNK test. Values associated with the same letter are not significantly different (P = 0.05).

	Root length (log. cm.)		
	P. lap.	P. pens.	P. pers.
Soil water content			
(c)	0.661^{u}	0.851^{wx}	0.817^{x}
(d)	0.944^{wz}	1.089^{y}	0.991^{vyz}
(e)	0.964^{vz}	1.087^{y}	1.009^{vyz}
(f)	0.903^{wxz}	1.066^{vy}	0.923^{wz}

Soil water contents (a) and (b) were not used in this experiment owing to poor seedling emergence.

For key to abbreviations see Appendix VI.1.

Appendix VI.7.

a) A summary of analysis of information on the numbers of plants flowering by the end of the experiment. Three species of Polygonum and four soil water contents were used in this experiment. Data from Experiment 1, Chapter VI.

Source of Information	D.F.	Information
Main effects		
Effect of soil water content.	3	74.976 **
(c) and (e) +	1	38.814 **
(e) and (f)	1	1.515 ns
(d) and (f)	1	3.459 ns
(d) and (e)	1	9.507 **
Effect of species	2	14.382 **
P. lap. - P. pens.	1	9.954 **
P. lap. - P. pers.	1	0.012 ns
P. pens. - P. pers.	1	10.766 **
Interaction	6	20.842 **
Joint Information	17	110.200 **

Experimental Error and Total Information not calculated as data consists of one replicate per treatment.

+ The difference between (c) and the closest value to it (e) was found to be significant ($P < 0.01$). On this basis differences between (c) and values for the other soil water contents were not made as they also were considered significantly different.

Appendix VI.7. (Continued)

b) Pairwise comparisons were made on the numbers of plants which flowered, between species and soil water content values, using information analysis. Values associated with the same letter are not significantly different ($P > 0.05$).

	Flowering (24 planted)		
	P. lap.	P. pens.	P. pers.
Soil water content			
(c)	0	0	0
(d)	19^{yz}	19^{yz}	18^{yz}
(e)	1	23^{z}	4^{x}
(f)	11^{xy}	19^{yz}	8^{x}

Low values cannot be accurately compared with other values unless their mean equals or is greater than 2 (Snedecor and Cochran 1967). Hence 0 and 1 cannot be compared, whereas 0,4 can (not significantly different, $P > 0.05$). 0 can be compared with all other values above 4 (significantly different, $P < 0.05$).

For key to abbreviations and symbols see Appendix VI.1.

Appendix VI.8. A summary of analysis of information on the numbers of pregerminated achenes emerged from different soils and sowing depths, using three species of smartweeds. Data from Experiment 2, Chapter VI.

Source of Information	D.F.	Information	
Main effects			
Effect of species	2	6.8044	*
P. lap. and P. pens.	1	6.4488	**
P. lap. and P. pers.	1	3.1574	ns
P. pens. and P. pers.	1	0.5046	ns
Effect of sowing depth	3	184.8471	***
surface and 1 cm. deep	1	1.1300	ns
surface and 2 cm. deep	1	7.0854	**
surface and 7.5 cm. deep	1	159.5928	***
1 cm. deep and 2 cm. deep	1	2.4766	ns
1 cm. deep and 7.5 cm. deep	1	134.7520	***
2 cm. and 7.5 cm. deep	1	101.9934	***
Effect of soil type	4	47.8263	***
Potting compost and clay	1	4.0138	*
Potting compost and sand	1	3.4152	ns
Potting compost and gravel	1	13.8968	***
Potting compost and lithosol	1	3.5282	ns
Clay and sand	1	0.0014	ns
Clay and gravel	1	32.7322	***
Clay and lithosol	1	15.1076	***
Sand and gravel	1	31.0016	***
Sand and lithosol	1	13.9310	***
Gravel and lithosol	1	3.4126	ns
Interaction			
species x sowing depth x soil type	24	235.5720	***
Joint Information	59	475.0498	***

Experimental Error and Total Information not calculated as data consists of one replicate per treatment.

Appendix VI.9.

a) Results of Bartlett's test on raw and transformed data obtained in Experiment 2, Chapter VI. This data consists of mean dry weights of plants of three species of Polygonum originally sown at four soil depths and in five soil types.

Calculated χ^2 values (adjusted) from Bartlett's tests			$\chi^2_{.01(41)}$ from tables
Raw data	Square root data	Log. data	
1274.083	423.078	109.908	66.206

Analysis of variance could not be used because of significant heterogeneity of variances. Multiple comparisons were therefore made using an approximate test of equality of means (Sokal and Rohlf 1969).

Weighted grand mean	Weighted correction term	Weighted S.S.	D.F.	Approx. F value
9.3343	2183.5309	3596.3358	207.159	82.3938 ***

From tables $F_{0.001(40,120)} = 2.11$

The null hypothesis that the samples were drawn from populations with equal means is rejected.

Mean dry weight, standard error and range is given for each treatment in VI.9b).

Appendix VI.9. (Continued)

b) Mean dry weights (g.) and 1 standard error of means for plants of *Polygonum lapathifolium*, *P. pensylvanicum* and *P. persicaria* planted at four depths and in five soil types. Data from Experiment 2, Chapter VI, see Fig. VI.5.

		P. lap.		P. pens.		P. pers.	
Soil type	Sowing depth	mean	S.E.	mean	S.E.	mean	S.E.
pc	surface	250.29	52.61	351.67	64.21	238.65	59.10
	1.0 cm.	189.52	36.97	207.95	57.66	265.93	51.53
	2.0 cm.	80.09	25.38	382.87	69.13	107.59	26.91
	7.5 cm.	p.s.s.		p.s.s.		p.s.s.	
cl	surface	30.07	6.76	49.27	7.53	37.73	6.47
	1.0 cm.	73.85	13.73	135.97	20.85	74.96	19.93
	2.0 cm.	46.38	7.16	120.27	22.49	50.17	14.95
	7.5 cm.	p.s.s.		80.69	24.27	124.64	12.85
sa	surface	4.70	1.82	5.37	1.23	7.58	3.11
	1.0 cm.	3.29	0.83	9.82	1.79	5.28	0.82
	2.0 cm.	5.67	0.90	12.76	2.50	9.07	3.55
	7.5 cm.	p.s.s.		p.s.s.		11.95	3.27
gr	surface	12.04	3.28	21.85	7.81	26.24	8.69
	1.0 cm.	p.s.s.		39.19	9.64	p.s.s.	
	2.0 cm.	p.s.s.		28.37	3.50	p.s.s.	
	7.5 cm.	p.s.s.		p.s.s.		p.s.s.	
li	surface	72.60	22.32	13.11	4.54	p.s.s.	
	1.0 cm.	7.47	1.51	27.38	6.63	20.37	4.83
	2.0 cm.	p.s.s.		22.87	4.70	23.23	5.83
	7.5 cm.	p.s.s.		p.s.s.		p.s.s.	

P. lap.	*P. lapathifolium*
P. pens.	*P. pensylvanicum*
P. pers.	*P. persicaria*
p.s.s.	poor seedling survival
pc	potting compost
cl	clay
sa	sand
gr	gravel
li	lithosol
S.E.	standard error of the mean

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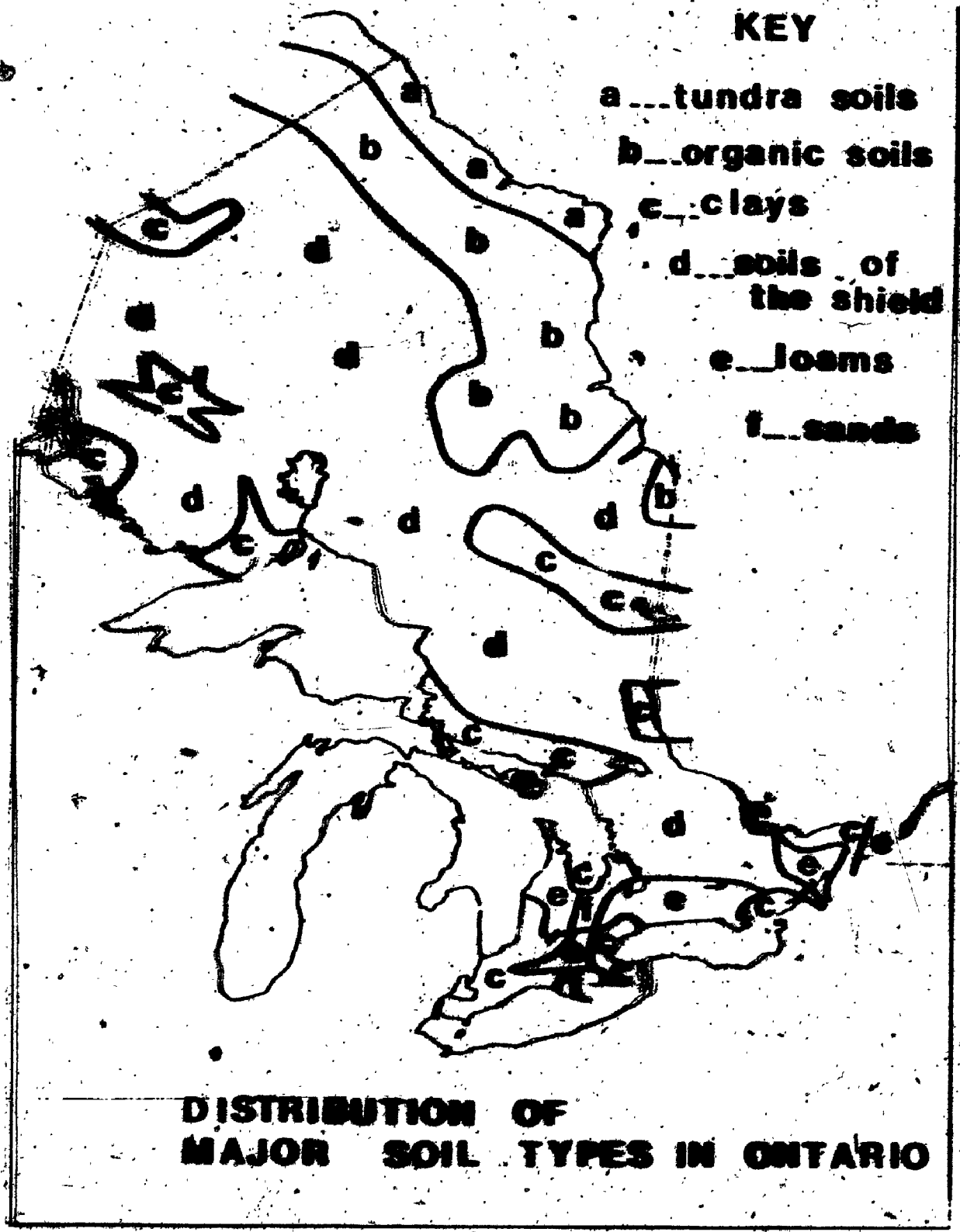
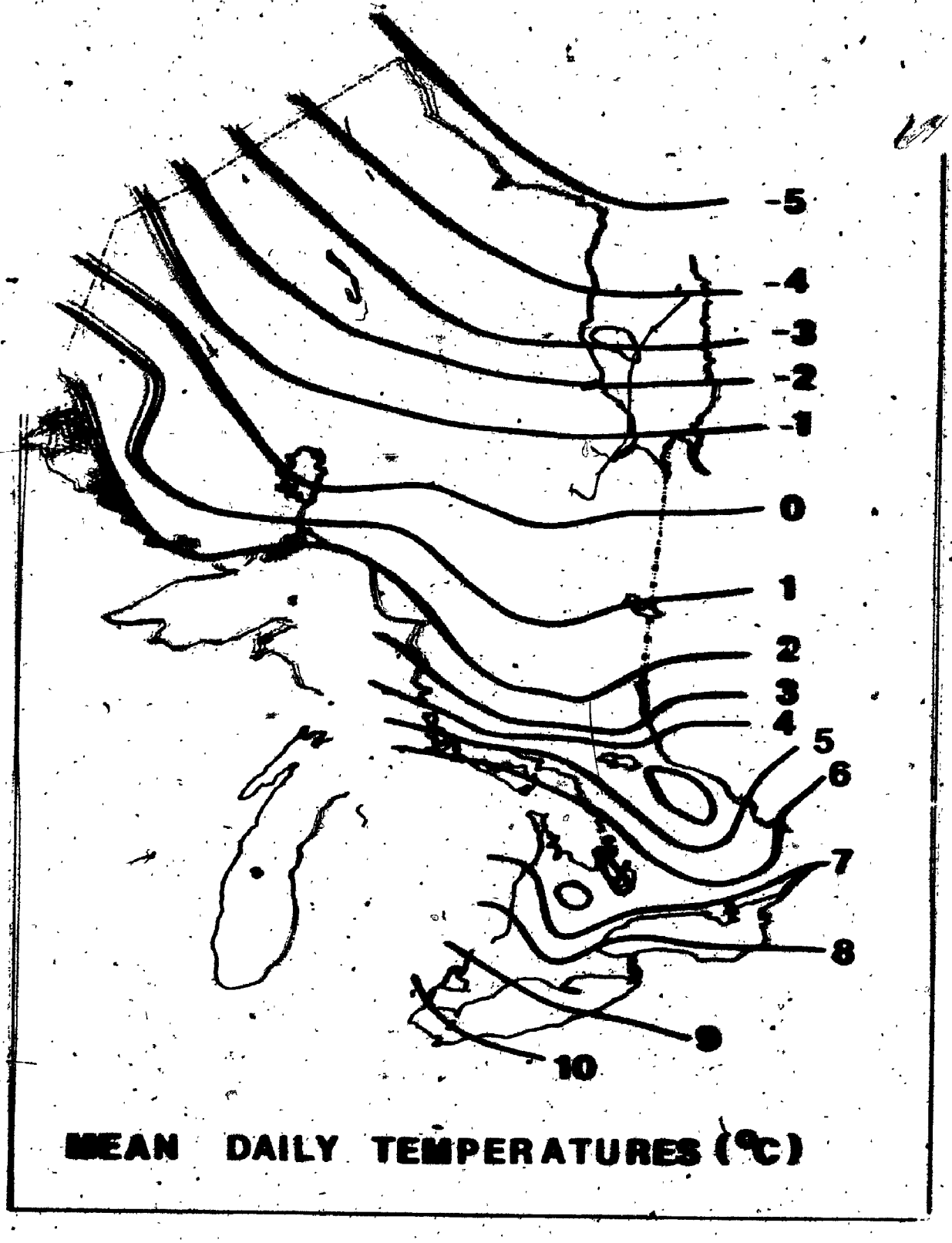


DISTRIBUTION OF MAJOR SOIL TYPES IN ONTARIO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MEAN DAILY TEMPERATURES (°C)