Phloem Transport in Plants

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To Professor Ernst Münch and other pioneers
in the field of plant physiology who,
by hard work, advanced this science to
its present level of sophistication.

Preface

The flow of sap and the distribution of foods in plants have presented some of the most challenging and baffling problems with which biologists have been faced. These problems were tackled by nearly every prominent plant physiologist of the nineteenth century—Hales, Hartig, von Mohl, Nageli, Sachs, and Strasburger, to mention only a few. More recently, Dixon, Curtis, Mason and Maskell, and Münch have made major contributions to this field.

During the past four decades, research on translocation in plants has gained momentum: the many recent papers cited in the bibliography of this book attest to the increased activity. The greatest progress has resulted from three types of study employing modern methods: (1) studies of phloem anatomy in which the electron microscope has been used to examine material prepared in such a way that sieve-plate plugging has been avoided, which have proven that the protoplasmic connections of the sieve plate are open tubules; (2) studies of phloem exudation, using aphids and excised aphid mouthparts, to determine the undisturbed velocities of flow, and the normal organic and inorganic composition, of the assimilate stream; and (3) studies of tracer movement, which have shown that many endogenous and exogenous materials move from sources to sinks, not along their own individual gradients, but along gradients of assimilates that are undergoing normal distribution in the organic nutrition of the plant.

Scientific progress is slow and painful. It is now more than one-

hundred-thirty years since Hartig (1837) first recognized and associated phloem transport with sieve-tube elements, through which the cellular foodstuffs are transported to all parts of the vascular plant. The electron microscopist has studied their structure, conformation, and distribution. The enzymologist has initiated work on the *in situ* biochemical systems and metabolic energy environs of phloem tissue, and the plant physiologist has brought into sharp focus the relationship of exudation and tracer transport to the direction and capacity of phloem translocation.

From these efforts emerges a mechanism to explain assimilate movement at all tissue levels in plants. The aim of this book is to collect and interpret the experimental information available on phloem transport in plants, not only to support the mechanism of assimilate movement, but to provide detailed analyses of the anatomy of the transport path itself, the phenomenon of phloem plugging, the movement of endogenous as well as xenobiotic compounds, the effects of environmental factors, and the complex quantitative aspects of assimilate distribution. More than this, there is now a rapidly growing body of evidence that the companion cell is not just another cell, but that it may, in fact, play a key role in phloem transport as a source of metabolic energy to maintain the integrity of the sieve tube plasmalemma. These interrelationships need considerably more study if we are fully to understand the energy balance between the various tissues and its relationship to long-distance transport in vascular plants. It may be that the answer to the controversy between the proponents of mass flow and those of energy-dependent systems lies in the mechanisms of energy-coupled respiration in the photosynthesizing tissue and the companion cells. In the final analysis we may learn to know and understand a unique molecular biology involving both systems.

We are indebted to our teachers, colleagues, and students, who helped guide our thinking toward the view of phloem transport that is embodied in this book. We are grateful to Rod Park and James Cronshaw for reading and critizing the manuscript. We thank Wanda Winton for skillful and efficient typing of the manuscript, and Mrs. R. Dial for careful collection of the bibliographic citations, and other assistance in preparing the book for publication. We, of course, are responsible for any errors or misinterpretations, and would be grateful if readers would call them to our attention. We would also welcome readers' suggestions for future studies of new principles and mechanisms.

October 1970

ALDEN S. CRAFTS
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Abbreviations and Trade Names

Å Ångstrom unit = 1×10^{-8} cm = 1×10^{-4} μ

abscisic acid 5-(1-hydroxy-2,6,6-trimethyl-4-oxo-2-cyclo-hexen-1-yl)-3-methyl-2,4-pentadienoic acid
(*syn.* dormin; abscisin II; ABA)

actinomycin D *N*,*N*′-{[2-amino-4,6-dimethyl-3-oxo-3*H*-phenoxazine-1,9-diyl]bis-[carbonylimino(2-hydroxypropylidene)-carbonylimino-isobutylidenecarbonyl-1,2-pyrrolidinediylcarbonyl(methylimino)-methylenecarbonyl]}bis-(*N*-methyl-L-valine)

acrolein 2-propenal

ADP adenosine 5′-(trihydrogen pyrophosphate)

a.e. acid equivalent

Alar mono(2,2-dimethylhydrazide)succinic acid
(*syn.* *N*,*N*-dimethylaminosuccinamic acid; Alar I; B9; B-995)

AMA methanearsonic acid, amine salts
(*syn.* methyldioxoarsenic acid, amine salts; amine methylarsonate)

amiben 3-amino-2,5-dichlorobenzoic acid

amiton *S*-[2-(diethylamino)ethyl]*O*,*O*-diethyl ester of phosphorothioic acid
(*syn.* *O*,*O*-diethyl *S*-2-diethylaminoethyl phosphorothioate; Chipman 6200)

amitrole 3-amino-*s*-triazole
(*syn.* 3-amino-1*H*-1,2,4-triazole; amino triazole; ATA)

AMO 1,618 (5-hydroxycarvacryl)trimethylammonium chloride, 1-piperidinecarboxylate
(*syn.* 2-isopropyl-4-dimethyl-amino-5-methylphenyl 1-piperidinecarboxylate-methochloride)

AMP adenosine 5′-(dihydrogen phosphate)

aniline blue 5,9-dianilino-7-phenyl-4,10-disulfobenzo[*a*]phenazinium hydroxide, inner salt

arthanitin fructosyl-cyclamiretin glucoside
(*syn.* cyclamine; primulin)

D-ascorbic acid D-*threo*-hex-2-enoic acid γ-lactone

ATP adenosine 5′-(tetrahydrogen triphosphate)

atrazine 2-chloro-4-(ethylamino)-6-(isopropylamino)-*s*-triazine

Azodrin® 3-hydroxy-*N*-methyl-*cis*-crotonamide, dimethyl ester with phosphoric acid

bacitracin A 4-{2-[2-(1-amino-2-methylbutyl)-2-thiazoline-4-carboxamido]-4-methylvaleramido}-*N*-(1-⟨{2-[3-aminopropyl]-8-benzyl-5-sec-butyl-14[(1-carbamoyl-2-carboxyethyl)carbamoyl]-11-[imidazol-4-ylmethyl]-3,6,9,12,16,23-hexaoxo-1,4,7,10,13,17-hexaazacyclotricos-22-yl}carbamoyl⟩-2-methylbutyl)glutaramic acid

BAP 6-benzylaminopurine
(*syn.* *N*-benzoyl-adenine; *N*-purin-6-yl-benzamide;BA)

barban *m*-chloro-carbanilic acid, 4-chloro-2-butynyl ester
(*syn.* 4-chloro-2-butynyl *N*-(3-chlorophenyl)carbamate; Carbyne®)

BECT di-(ethylxanthogen) trisulfide
(*syn.* Defoliant 713)

Bidrin® 3-hydroxy-*N*,*N*-dimethyl-*cis*-crotonamide, dimethyl ester with phosphoric acid
(*syn.* 3-(dimethoxyphosphinyloxy)-*N*,*N*-dimethyl-*cis*-crotonamide)

biopterin 1-(2-amino-4-hydroxy-6-pteridinyl)-1,2-propanediol
(*syn.* 2-amino-4-oxy-6-(1,2-dioxypropyl)-pteridine; L-*erythro*-(biopterin); crithidia factor)

bromphenol blue 4,4′-(3*H*-2,1-benzoxathiol-3-ylidene)bis-2-bromo-6-chlorophenol

BTP 6-(benzylamino)-9-(2-tetrahydropyranyl)-9*H*-purine

CCC (2-chloroethyl)trimethyl ammonium chloride
(*syn.* Cyocel 1; chlorocholine chloride)

CF1 2-chloro-9-hydroxyfluorene-9-carboxylic acid
(*syn.* Chlorflurenol)

chloramphenicol D-*threo*-(−)-2,2-dichloro-*N*-[β-hydroxy-α-(hydroxymethyl)-*p*-nitrophenylethyl] acetamide
(*syn.* Chloromycetin)

chlorphenol red 4,4′-(3*H*-1,2-benzoxathiol-3-ylidene)-bis-2-chlorophenol

CIPC *m*-chlorocarbanilic acid, isopropyl ester
(*syn.* isopropyl-*N*-(3-chlorophenyl)-carbamate)

count/min counts per minute
(*syn.* CPM)

cP centipoise

CPA 4-chlorophenoxyacetic acid
(*syn.* Tomatotone)

cycloheximide 3-[2-(3,5-dimethyl-2-oxocyclohexyl)-2-hydroxyethyl]-glutarimide
(*syn.* isocycloheximide; Actidione)

D-1991 (1-butylcarbamoyl)-2-benzimidazolecarbamic acid

2,4-D 2,4-dichlorophenoxyacetic acid

dalapon 2,2-dichloropropionic acid, sodium salt

2,4-DB 2,4-dichlorophenoxybutyric acid

DCPA 2,3,5,6-tetrachloroterephthalic acid, dimethyl ester
(*syn.* Dacthal®)

DDS bis(4-aminophenyl)sulfone

DDT 1,1,1-trichloro-2,2-bis(*p*-chlorophenyl)ethane

dehydroascorbic acid D-*threo*-2,3-hexodiulosonic acid, γ-lactone

2,4-DI 2,4-dichloro-5-iodophenoxyacetic acid

di-allate diisopropylthiolcarbamic acid, *S*-(2,3-dichloroallyl)ester
(*syn.* *S*-2,3-dichloroallyl *N*,*N*-diisopropylthiolcarbamate; DATC; Avadex®)

dicamba 3,6-dichloro-*o*-anisic acid
(*syn.* Banvel D®; mediben)

dihydrostreptomycin *O*-2-deoxy-2-(methylamino)-α-L-glucopyranoxyl-(1→2)-*O*-5-deoxy-3-*C*-(hydroxymethyl)-α-L-lyxo-furanosyl-(1→4)-*N*,*N*′-diamidino-streptamine
(*syn.* Didromycine®)

diketogulonic acid L-*threo*-2,3-hexodiulosonic acid, γ-lactone

dimefox *N*,*N*,*N*′,*N*′-tetramethylphosphorodiamidic fluoride
(*syn.* bis(dimethylamido)phosphoryl fluoride; DMF; Pestox 14)

dimethoate 2-mercapto-*N*-methylacetamide phosphorodithioic acid, *O*,*O*-dimethyl ester with *S*-ester
(*syn.* Rogor®; Cygon®)

diquat 6,7-dihydrodipyrido[1,2-*a*:2′,1′-*c*]pyrazinediium dibromide
(*syn.* 1:1′-ethylene-2′,2′-dipyridylium dibromide; Regulone®)

disulfoton *O*,*O*-diethyl-*S*-[2-(ethylthio)ethyl]ester of phosphorodithioic acid
(*syn.* Di-Syston®)

diuron 3-(3,4-dichlorophenyl)-1,1-dimethylurea
(*syn.* DCMU)

DNA deoxyribonucleic acid

DNBP 2,4-dinitrobutylphenol

DNOC 3,5-dinitro-*o*-cresol

DNP 2,4-dinitrophenol

2,4-DP 2-(2,4-dichlorophenoxy)propionic acid
(*syn.* dichlorprop)

DPN 3-carbamoyl-1-ribofuranosyl-pyridinium hydroxide, (5′→5′) ester with adenosine 5′-(trihydrogen pyrophosphate), inner salt
(*syn.* nicotinamide adenine dinucleotide, oxidized; diphosphopyridine nucleotide; NAD)

DPNH adenosine 5′-(trihydrogen pyrophosphate), (5′→5′) ester with 1,4-dihydro-1-α-D-ribofuranosylnicotinamide
(*syn.* nicotinamide adenine dinucleotide, reduced; diphosphopyridine nucleotide, reduced; NADH)

DSMA methanarsonic acid, disodium salt

DTPA diethylenetriaminepentaacetate

Duraset® *N*-*meta*-tolyl phthalamic acid
(*syn.* 7R5)

EDTA ethylenediaminetetraacetic acid, tetrasodium salt
(*syn.* (ethylenedinitrilo)tetraacetic acid, tetrasodium salt)

EHPG *N*,*N*′-ethylene-bis-[2-(*O*-hydroxyphenyl)]glycine

endothall 7-oxybicyclo[2.2.1]heptane-2,3-dicarboxylic acid
(*syn.* 3,6-endoxyhexahydrophthalic acid)

endrin 1,2,3,4,10,10-hexachloro-6,7-epoxy-4a,5,6,7,8,8a,9,9-octahydro-1,4-*endo*-5,8-*endo*-dimethanonaphthalene

endrin-ketone 1,2,3,4,10,10-hexachloro-6,7-epoxy-4a,5,6,7,8,8a-hexahydro-1,4-*endo*-5,8-keto-dimethanonaphthalene

eosine Y 2′,4′,5′,7′-tetrabromo-9-(*o*-carboxyphenyl)-6-hydroxy-3*H*-xanthene-3-one,3′,6′-dihydroxyfluoran
(*syn.* 2′,4′,5′,7′-tetrabromofluorescein)

EPTC ethyl-di-*n*-propylthiolcarbamate
(*syn.* Eptam®)

erythrosine 2′,4′,5′,7′-tetraiodo-9-(*o*-carboxyphenyl)-6-hydroxy-3*H*-xanthene-3-one,3′,6′-dihydroxyfluoran
(*syn.* 2′,4′,5′,7′-tetraiodofluorescein)

FAP 6-furfurylaminopurine
(*syn.* *N*-furfuryladenine)

fenac 2,3,6-trichlorophenylacetic acid

FL 9-hydroxyfluorene-9-carboxylic acid
(*syn.* Flurenol)

fluometuron 3-(*m*-trifluoromethylphenyl)-1,1-dimethylurea
(*syn.* Cotoran®)

fluorescein-K 9-(*o*-carboxyphenyl)-6-hydroxy-3*H*-xanthene-3-one,3′,6′-dihydroxyfluoran, potassium salt
(*syn.* resorcinolphthalein, potassium salt; uranine, potassium salt; Uranine Yellow, potassium salt)

ft-c foot-candle

folic acid *N*-⟨*p*-{[(2-amino-4-hydroxy-6-pteridinyl)methyl]amino}benzoyl⟩-L-glutamic acid
(*syn.* pteroylmonoglutamic acid)

gibberellin 2β,4a,7-trihydroxy-1-methyl-8-methylene-4aα,4bβ,-gibb-3-ene-1α,10β-dicarboxylic acid,1,4a-lactone
(*syn.* gibberellic acid; GA_3)

griseofulvin 7-chloro-2′,4,6-trimethoxy-6′β-methyl-spiro[benzofuran-2(3*H*),1′-[2]cyclohexene]3,4′-dione

GTP guanosine-5′-(tetrahydrogen triphosphate)

^3H_2O $^3H—O—^3H$
(water completely labeled with tritium)

HTO H—O—^3H
(water half labeled with tritium)

IAA indol-3-acetic acid
(*syn.* heteroauxin)

INBA 2-iodo-4-nitrobenzoic acid

ioxynil 3,5-diiodo-4-hydroxybenzonitrile

IPC carbanilic acid, isopropyl ester
(*syn.* isopropyl *N*-phenylcarbamate)

Irgafen N^1-(3,4-dimethylbenzoyl)-sulfanilamide

isolan 1-isopropyl-3-methylpyrazol-5-yl ester of dimethylcarbamic acid
(*syn.* dimethyl-5-(1-isopropyl-3-methylpyrazolyl)carbamate)

ITP inosine 5′-(tetrahydrogen triphosphate)

maleic hydrazide 1,2-dihydro-3,6-pyridazinedione
(*syn.* 6-hydroxy-3(2*H*)-pyridazinone; MH)

MCPA 4-chloro-2-methylphenoxyacetic acid
(*syn.* [(4-chloro-*o*-tolyl)oxy]-acetic acid)

MCPB 4-chloro-2-methylphenoxybutyric acid

menazon *S*-[(4,6-diamino-*s*-triazin-2-yl)-methyl],*O*,*O*-dimethyl esters of phosphorodithioic acid

mercurochrome 2′,7′-dibromo-4′-(hydroxymercurio)-9-(*o*-carboxyphenyl)-6-hydroxy-3*H*-xanthen-3-one,3′,6′-dihydroxyfluoran, disodium salt
(*syn.* 2,7-dibromohydroxymercurifluorescein, disodium salt)

methyl demeton mixture of *O,O*-dimethyl-*O*-2(ethylthio)ethyl phosphorothioate and *O,O*-dimethyl-*S*-2(ethylmercaptoethyl)-dimethyl thionophosphate

Mev million electron volts

monuron 3-(*p*-chlorophenyl)-1,1-dimethylurea

MOPA 3-methoxyphenylacetic acid

myoinositol 1,2,3,4,5,6-cyclohexanehexol
(*syn. meso*-inositol)

NAA 1-naphthalenacetic acid

NAD *see* DPN

NADH *see* DPNH

NADP *see* TPN

NADPH *see* TPNH

naptalam *N*-1-naphthylphthalamic acid
(*syn.* Alanap)

Nellite® *N,N'*-dimethylphosphorodiamidic acid, phenyl ester
(*syn.* phenyl-*N,N'*-dimethylphosphordiamidate)

neomycin A 2-deoxy-4-*O*-(2,6-diamino-2,6-dideoxy-α-D-glucopyranosyl)-D-streptamine
(*syn.* Neamine)

nicotinic acid 3-pyridinecarboxylic acid

oligomycin Rutamycin (an antibiotic substance)

oxamycin D-4-amino-3-isoxazolidone

P poise

paraquat 1,1'-dimethyl-4,4'-dipyridylium cation

pantothenic acid *N*-(2,4-dihydroxy-3,3-dimethylbutyryl)-β alanine

PCP pentachlorophenol

phlorizin 3,5-dihydroxy-2-(*p*-hydroxyhydrocinamoly)phenyl β-D-glucopyranoside
(*syn.* phloridzin)

Phosdrin® 2-carbomethoxy-1-propen-2-yl-dimethyl phosphate
(*syn. O,O*-dimethyl-1-carbomethoxy-1-propen-2-yl phosphate; mevinphos)

phosphamidon 1-chloro-1-diethylcarbamoyl-1-propen-2-yl dimethyl phosphate
(*syn.* dimethyl-diethylamido-1-chlorocrotonyl[2]phosphate)

phosphon 2,4-dichlorobenzyltributylphosphonium chloride
(*syn.* phosphon D)

picloram 4-amino-3,5,6-trichloropicolinic acid
(*syn.* Tordon®)

Pleocidin® an antibiotic substance

polyoxin 1-[5-(2-amino-2-deoxy-L-xylonamido)-6-*C*-(2-carboxy-3-ethylidene-1-azetidinyl)-5-deoxy-β-D-*allo*-hexodialdo-1,4-furanosyl]-5-(hydroxymethyl)-uracil
(*syn.* Polyoxin-A®)

P-protein phloem protein

P1-protein protein component of sieve-tube slime with tubules 231 Å in diameter

P2-protein protein component of sieve-tube slime with tubules 149 Å in diameter

prometryne 2,4-bis(isopropylamino)-6-(methylthio)-*s*-triazine

propanil 3,4-dichloropropionanilide
(*syn.* DPA)

Pyrazoxon® *O*,*O*-diethyl-*O*-(3-methyl-5-pyrazolyl) phosphate

pyridoxine 5-hydroxy-6-methyl-3,4-pyridinedimethanol

R_f in chromatography, the distance traveled by a given substance divided by the distance traveled by the solvent front

RH relative humidity

rhodamine B [9-(2-carboxy-4-isothiacyanatophenyl)-6-diethylamino-4-3*H*-xanthen-3-ylidene] diethyl ammonium

rhodamine 6G *o*-[6-(ethylamino)-3-(ethylimino)-2,7-dimethyl-3*H*-xanthen-9-yl] benzoic acid

riboflavin 7,8-dimethyl-10-(D-ribo-2,3,4,5-tetrahydroxypentyl)isoalloxazine

RNA ribonucleic acid

RQ respiratory quotient

schradan bis-*N*,*N*,*N*′,*N*′,-tetramethylphosphorodiamidic anhydride
(*syn.* OMPA)

silvex 2-(2,4,5-trichlorophenoxy)propionic acid

simazine 2-chloro-4,6-bis(ethylamino)-*s*-triazine

streptomycin *O*-2-deoxy-2-(methylamino)-α-L-glucopyranosyl-(1→2)-*O*-5-deoxy-3-*C*-formyl-α-L-lyxofuranosyl-(1→4)-*N*,*N*′-diamidino-D-streptamine

streptothricin 2-{[2-(3-amino-6-{3-amino-6-[3-amino-6-(3,6-diaminohexanamido)hexanamido]-hexanamido}-hexanamido)-2-deoxy-α-D-gulopyranosyl]amino}-3,3a,5,6,7,7a-hexahydro-7-hydroxy-4*H*-imidazol(4,5-*C*)pyridin-4-one

Systox® *O,O*-diethyl-*O*-[2-(ethylthio)ethyl] ester mixed with *O,O*-diethyl-*S*-[2-(ethylthio)ethyl] ester of phosphorothioic acid (*syn.* demeton; demeton O + demeton S)

T-1947 polyoxyethylene-polyoxypropylene-polyol

2,4,5-T 2,4,5-trichlorophenoxyacetic acid

TBA 2,3,6-trichlorobenzoic acid

TCPP 1,3,5-tricyano-3-phenylpentane

Temik® 2-methyl-2-(methylthio)propionaldehyde *O*-(methylcarbamoyl)-oxime

tetramine 2,2,6,6-tetraoxide of 2,6-dithia-1,3,5,7-tetraazaadamantane

thiamine {3-[(4-amino-2-methyl-5-pyrimidinyl)-methyl]-5-(2-hydroxyethyl)-4-methylthiazolium}chloride

thiazamide N^1-2-thiazolylsulfanilamide

Thimet® *O,O*-diethyl-S-[(ethylthio)methyl] ester of phosphorodithioic acid

TIBA 2,3,6-triiodobenzoic acid

TPA 2,2,3-trichloropropionic acid

TPN 3-carbamoyl-1-β-D-ribofuranosylpyridinium hydroxide, (5′→5′) ester with adenosine 2′-(dihydrogen phosphate)5′-(trihydrogen pyrophosphate), inner salt (*syn.* nicotinamide adenine dinucleotide phosphate, oxidized; triphosphopyridine nucleotide; NADP)

TPNH 2′-(dihydrogenphosphate)5′-(trihydrogen pyrophosphate), (5′→5′) ester with 1,4-dihydro-1-β-D-ribofuranosylnicotinamide (*syn.* nicotinamide adenine dinucleotide phosphate, reduced; triphosphopyridine nucleotide, reduced; NADPH)

Tween 20 polyoxyethylene sorbitan monolaurate

Tween 80 polyoxyethylene sorbitan monooleate

UDP uridine 5′-(trihydrogen pyrophosphate)

UDPG mono-α-D-glucopyranosyl ester of uridine 5′-(trihydrogen pyrophosphate)

UMP 5′-uridylic acid

UTP uridine 5′-(tetrahydrogen triphosphate)

vitamin B_{12} cobinamide cyanide hydroxide dihydrogen phosphate (ester) inner salt 3′ ester with 5,6-dimethyl-1-α-D-ribofuranosylbenzimidazole

UV ultraviolet

X-77 a blended surfactant containing alkylarylpolyoxyethylene glycols, free fatty acids, and isopropanol

Contents