Time-dependent Behavior of a Mathematical Model for Munch Translocation

APPLICATION TO RECOVERY FROM COLD INHIBITION

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ABSTRACT

The time evolution of a Munch pressure-flow translocation system is calculated using a numerical computer method. Results are obtained for the time course of the system variables following application of a large resistance in the translocation path, intended to simulate a cold block. The resistance factor required to produce translocation inhibition indicates that even moderate inhibition is primarily due to sieve plate pore blockage, rather than to the viscosity increase. The calculated time for recovery from cold inhibition and the shape of the translocation recovery curve agree with experimental results. The time for translocation recovery and the level of velocity recovery depend on the rate of sucrose unloading in the sink; on the sucrose concentration in the sieve tube; on the position, length, and resistance factor of the cold block; and on the hydraulic conductivities.

There have been a number of mathematical treatments of Munch's pressure-flow hypothesis for phloem translocation (1, 2, 6–8). The quantitative results for steady state translocation support the possibility of Munch translocation in sugar beet and other plants (1, 6). We have obtained a time-dependent solution in order to further test the Munch hypothesis.

THE MODEL

We use the general mathematical model for Munch translocation as described in a previous paper (1). The difference between the present numerical calculation, which gives a time-dependent solution of the model, and the previous calculation, which gave only the steady state, follows. In the present calculation, for every time increment, sucrose is loaded into the translocation system in the source region and unloaded in the sink (via equation 6, ref. 1); the other model equations are then iterated 10 to 20 times until a self-consistent set of variables (sucrose concentration, hydrostatic pressure, water influx, and solution velocity in the sieve tube) are obtained. This process is repeated, yielding the time evolution of the system.

This time-dependent solution is used to obtain the theoretical time-dependent behavior of a Munch translocation system following application of a large resistance increase in the translocation path of a system originally at steady state, intended to simulate application of a cold block. In the computer calculation, the Munch translocation process is broken down into time intervals of 1 sec and space intervals of either 0.6 or 2.4 cm. The measured sieve tube dimensions and translocation rate for sugar beet are used, as given in reference 1. The specific mass transfer rate is 7.5 g hr^{-1} cm^{-2}. We use model II of reference 1, with active loading into companion cells, since this model is supported by recent experimental work (3). For the lateral membrane conductivity we use, unless otherwise specified: $L_p = 2.2 \times 10^{-7}$ cm sec^{-1} atm^{-1}, and for sieve-tube conductivity in the path, per sieve-tube element: $L_s = 10.2$ cm sec^{-1} atm^{-1}. A 2.4-cm cold block, a 19.2-cm path, and a 9.6-cm source and sink are used unless otherwise specified.

It should be noted that the numerical solution process is greatly speeded up by using the difference between the two calculated values of water influx which the model provides to increment the hydrostatic pressure uniformly along the sieve tube in such a way as to reduce this difference by a factor of two. About 1 min of computer time on an IBM 370/165 is required to produce the time evolution of the system for 3 hours. A complete Fortran program deck is available to anyone interested in the details.

The data of Giaquinta and Geiger (5) show that inhibition by a cold block in the translocation path in sugar beet is characterized by a "critical temperature" of about 0 C, above which recovery occurs in less than 90 min, with a Q_{10} of 1.5 for the translocation rate 10 min after application of the cold block (approximately the minimum of translocation). Thus, at 11 C, the minimum translocation rate is about 54% of the preinhibition rate (at 26 C), and at 6 C the minimum rate is about 44%. The experiments used a 2-cm cold block on the source leaf petiole, with about a 20-cm path. It should be noted that the velocity as well as the translocation rate recovers completely in these experiments.

In order to simulate the effect of the cold block above the critical temperature, it was found that a resistance increase (a decrease in L_s) in the range of 50 to 200 times normal was required in the cold block. A resistance increase this large cannot be accounted for by the viscosity increase, but would have to be due to sieve plate pore blockage.

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RESULTS

The model recovery time is found to depend on: (a) the unloading rate in the sink, (b) the over-all sucrose concentration level, (c) the position, length, and resistance factor of the cold block, and (d) the values of the parameters L_s and L_p. Recovery time is only slightly dependent on the cross-sectional area of the sieve tube and the lateral surface area of the sieve tube and companion cells. The recovery time is not sensitive to changes in the water potential of the surrounding reservoir. An increase in surrounding water potential results in an equal increase in sieve tube hydrostatic pressure, with no changes in system behavior. A substantial change in surrounding water potential gradient produces only a small change in translocation recovery time.

It should be pointed out that the over-all sucrose concentration level is not uniquely determined by the parameters. A careful analysis of the model equations shows that, although there are four equations and four variables for each section, except at the ends, there is one more variable than independent equation for the entire system. This allows the concentration in one section to be arbitrary, subject to physical limitations. In the present calculations, the preinhibition steady state concentration level is determined by the level of the uniform concentration in the initial state from which the steady state is obtained. The previously reported steady state results (1) represent translocation with the minimum sucrose concentration possible for the given parameters.

The model results agree with the experimental results, in that an inhibition of translocation to about 40% of the steady state rate is followed by complete recovery in less than 90 min. The calculated average velocity does not show complete recovery in all cases. The calculated average velocity, intended to be analogous to the measured velocity (4), is meaningful only at steady state, where it is equal to the length of the path and half of the sink, divided by the time required for a volume element of solution to traverse that length. In general, the calculated recovery of the translocation rate is faster when the unloading rate is higher, when the cold block is closer to the source, or when the length or resistance factor of the cold block is less. The recovery of average velocity is more complete when the unloading rate is higher, or when the cold block is closer to the source. These results are illustrated in Table I. Some representative calculated recovery curves are shown in Figure 1.

An apparent exception to the general tendency for the re-

Table I. *Time Required for 80% and 99% Translocation Rate Recovery*

Results are given in minutes (t), percentage level of average velocity recovery at 90 min after application of cold block (r), and minimum translocation rate as percentage of steady state rate (m). Cold block length = 2.4 cm.

Concn at source end (μg cm^{-3} X 10^{-4})·	31.6	32.7	22.3	24.0	14.0	14.0
Average velocity (cm min^{-1})	0.42	0.40	0.63	0.58	1.28	1.28
Unloading	b[1]	a[2]	b	a	b	a

Cold Block Location and Resistance Factor						
CBR[3] factor = 100						
Near source						
t	4; 22	17; 43	6; 28	22; 52	31; 90	29; 64
r	105	95	109	91	76	76
m[4]	75(1)92	40(4)60	75(2)87	41(5)51	61(12)61	44(9)44
Near sink						
t	9; 27	32; 80	13; 36	39; 93	49; 149	47; 117
r	100	83	100	74	50	50
m[4]	41(1)82	20(2)41	38(1)72	20(2)35	32(2)36	20(4)26
CBR factor = 200						
Near source						
t	7; 36	28; 66	11; 44	33; 74	45; 122	41; 86
r	109	91	116	85	68	68
m[4]	72(2)84	27(5)39	72(2)79	29(6)33	50(15)53	33(11)33
Near sink						
t	17; 47	53; 125	34; 105	61; 138	73; 194	70; 163
r	101	73	80	62	39	39
m[4]	34(1)65	11(2)25	32(1)54	12(3)20	22(8)23	13(6)15
CBR = 100; L_s corrected for viscosity factor						
Near source						
t	6; 37	51; >300	6; 35	32; 84	30; 117	31; 75
r	109	77	112	86	74	74
m[4]	75(2)85	33(5)40	75(2)85	38(6)43	64(11)64	45(8)46
Near sink						
t	13; 36	92; >300	13; 35	57; 152	49; 180	48; 140
r	101	61	100	65	49	48
m[4]	37(1)72	15(2)27	37(1)72	19(3)30	34(1)42	23(4)30

[1] b: unloading rate = preinhibition unloading rate.
[2] a: unloading rate = rate of entry of sucrose into sink.
[3] CBR: cold block resistance.
[4] Minimum rate (time following application of cold block at which minimum occurs) rate at 10 min.
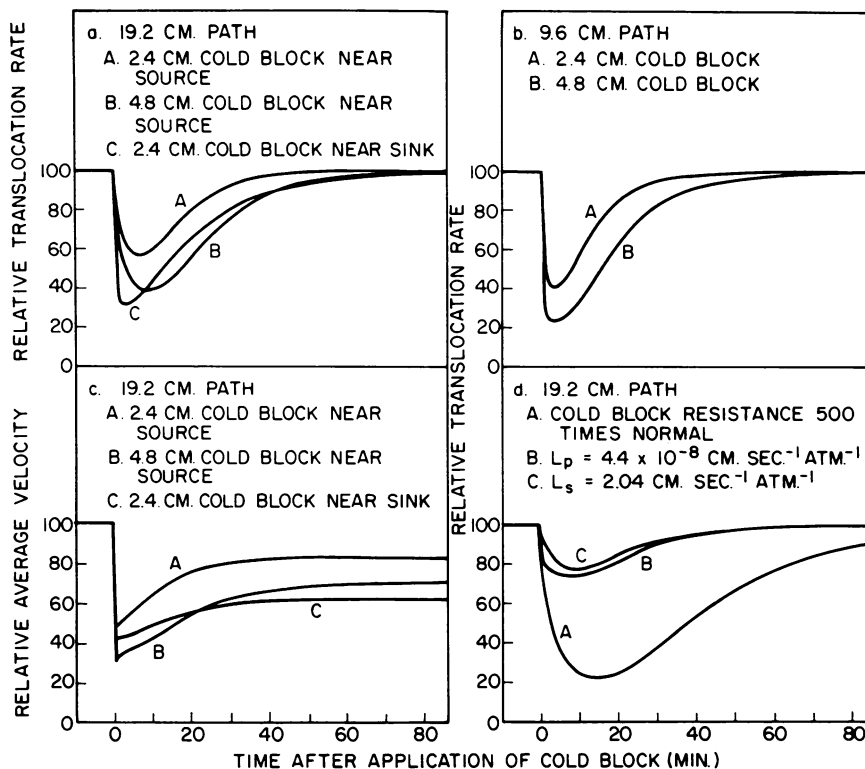
FIG. 1. Recovery curves for translocation rate into sink and for average solution velocity. Unless otherwise indicated, $L_p = 2.2 \times 10^{-7}$ cm sec^{-1}atm^{-1}, $L_s = 10.2$ cm sec^{-1} atm^{-1} per sieve tube element in the path, and cold block resistance factor $= 50$. The unloading rate per section in the sink is set at the rate of sucrose entry into the sink divided by the number of sections in the sink. a: Preinhibition sucrose concentration at the source end of the sieve tube is $1.4 \times 10^5 \, \mu g$ cm^{-3}. Cold block near source begins 2.4 cm from source, and cold block near sink ends 2.4 cm from sink. b: Cold block begins 2.4 cm from source; c: preinhibition steady state average velocity is 1.28 cm min^{-1}; d: cold block is 2.4 cm long, 2.4 cm from source, with a 19.2 cm path. The response with a 2.4-cm cold block and a resistance factor of 100 is similar to that shown here with a 4.8-cm cold block and a resistance factor of 50.

covery time to be lower for a higher unloading rate is shown in Table I for cases with the lowest concentration. However, in these cases, with unloading rate initially equal to the preinhibition rate, the concentration in the sink decreases to a near zero level, the concentration gradient becomes zero in the last half of the sink, and unloading can be maintained only at a very low rate, resulting in a long recovery time. In the present calculations, a lower limit on concentration is set at $1 \times 10^4 \, \mu g$ cm^{-3}.

The mechanism of translocation recovery as given by the model is shown in Figure 2. There is a buildup of sucrose on the source side of the cold block, producing a buildup of hydrostatic pressure gradient across the cold block. The increase in concentration extends slightly beyond the cold block, resulting in a large influx of water in a short region on the sink side of the cold block, allowing the velocity on the sink side of the cold block to build up to or exceed the preinhibition velocity.

DISCUSSION

Since velocity on the source side of the cold block is lower after recovery than before inhibition (due to the higher concentration there), average velocity can recover completely only if there is a draw down of sucrose on the sink side of the cold block, allowing the velocity there to go above the preinhibition level. Such a draw down occurs with a higher unloading rate, which in turn leads to a faster buildup of a large osmotic pressure gradient across the cold block, resulting in a faster buildup of hydrostatic pressure gradient and faster recovery.

The preinhibition unloading rate constitutes an upper bound for the unloading rate during inhibition and recovery, inasmuch as it is unreasonable to assume that the unloading rate would increase as the amount of sucrose moving into the sink region decreases. If unloading is maintained at the preinhibition level, the concentration in the sink will decrease during recovery. However, it is reasonable to assume that a decrease in concentration would lead to a decrease in unloading rate. If the unloading rate goes below the rate of sucrose entry into the sink region, the sink concentration will increase, leading to an increase in unloading rate. Thus, an unloading rate equal to the rate of sucrose entry into the sink is a lower bound for the unloading rate. Such an unloading rate during the entire course of recovery will maintain the sink concentration at the preinhibition level.

As shown by the model results in Table I, the over-all concentration level has a considerable effect on the recovery time. A higher over-all concentration level requires a lower velocity and thus a lower hydrostatic pressure gradient, which would result in a lower recovery time. However, if the effect of increased concentration on viscous resistance is taken into account, the difference in steady state hydrostatic pressure gradient for different concentrations is reduced. This effect, plus the further increase in resistance as the concentration builds up during recovery, results in a recovery time which increases with concentration.

When the cold block is closer to the source, there is a shorter region with the velocity decrease which accompanies the concentration increase, and hence there is a more complete recovery of average velocity. The shorter region of tube in which the concentration must build up results in faster recovery of both translocation rate and average velocity.
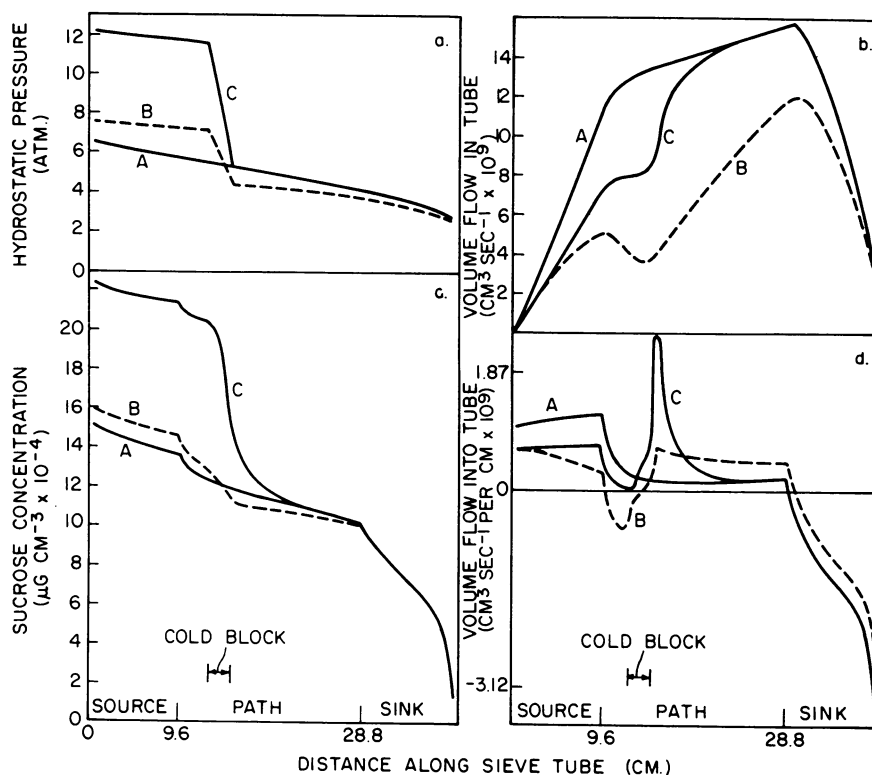
FIG. 2. System variables as a function of position along the sieve tube. A: Preinhibition steady state; B: 1 min after application of cold block; C: steady state following recovery of translocation rate, with cold block. The cold block resistance factor is 50, and the standard values for L_p and L_s are used.

If either L_s or L_p is increased, there is relatively little effect on the recovery characteristics. If either of these parameters is decreased, there is some effect, as seen in Figure 1. This effect is carried out with a constant cold block resistance; the cold block resistance factor is decreased in proportion to the decrease in L_s. The effect of a change in L_s is similar to the effect of a change in L_p. This similarity exists because, for the values of the parameters used here, the total conductivity of the sieve tube (approximately equal to L_s multiplied by the cross-sectional area divided by the total number of elements) happens to be about equal to the total conductivity of the lateral surface of the system (approximately equal to L_p multiplied by the total surface area of the source region divided by 2).

The data of Geiger et al. (3) show a solute concentration corresponding to 3.9 to 4.2×10^5 μg cm^{-3} of sucrose in sugar beet source leaf sieve tubes, and 3.1 to 3.5×10^5 μg cm^{-3} in the sink leaf sieve tubes. If this concentration is all sucrose, the present model would require an average velocity of less than 0.4 cm min^{-1}. The measured velocity in sugar beet of about 1 cm min^{-1} (4, 5) is more consistent with the model results for concentrations of about 1.7×10^5 μg cm^{-3} in the source. It may be that the translocation rate used in the model calculation is too low. However, the osmotic pressure in the actual sieve tube is almost certainly not entirely due to sucrose. A constant and uniform osmotic pressure could be added to that due to sucrose in the present model with no change in model behavior. This pressure could represent some other solute that does not contribute to the osmotic pressure gradient being transported along with sucrose, or it could represent a matric pressure due to anchored material in the sieve tube, such as P-protein.

In order to provide a more definitive test of the proposed mechanism for recovery, data on sucrose concentrations before inhibition and after recovery would be useful, as would experiments on the effect of cold block position. The present results provide some insights into this mechanism, and the agreement with experimental results provides some support for the validity of the mechanism.

Note Added in Proof. Although it has only a very small effect, the term αV_i $(C_i(t + \Delta t) - C_i(t))/\Delta t$ should be added to the left side of equation 4 in reference 1, and also to the numerator on the right side of equation 5. Alternatively, equations 4 and 5 can be simplified by replacing all $1 - \alpha C$ factors by 1, and adding αr_i to the left side of equation 4 and to the numerator on the right side of equation 5. We use $\alpha = 6.0 \times 10^{-7}$ cm^3 μg^{-1}. For viscosity (in poise), we use $\eta_i = 9.0 \times 10^{-3} + 1.7 \times 10^{-13} C_i C_{i+1} + 5.7 \times 10^{-13}$ $(C_i - 3.6 \times 10^5)^2$. The last term is deleted for C_i less than 3.6×10^5 μg cm^{-3}.

LITERATURE CITED

1. CHRISTY, A. L. AND J. M. FERRIER. 1973. A mathematical treatment of Munch's pressure-flow hypothesis of phloem translocation. Plant Physiol. 52: 531–538.
2. ESCHRICH, W., R. F. EVERT, AND J. H. YOUNG. 1972. Solution flow in tubular semipermeable membranes. Planta 107: 279–300.
3. GEIGER, D. R., R. T. GIAQUINTA, S. A. SOVONICK, AND R. J. FELLOWS. 1973. Solute distribution in sugar beet leaves in relation to phloem loading and translocation. Plant Physiol. 52: 585–589.
4. GEIGER, D. R. AND S. A. SOVONICK. 1970. Temporary inhibition of translocation velocity and mass transfer rate by petiole cooling. Plant Physiol. 46: 847–849.
5. GIAQUINTA, R. T. AND D. R. GEIGER. 1973. Mechanism of inhibition of translocation by localized chilling. Plant Physiol. 51: 372–377.
6. TYREE, M. T., A. L. CHRISTY, AND J. M. FERRIER. 1974. A simpler iterative steady state solution of Munch pressure-flow systems applied to long and short translocation paths. Plant Physiol. 54: 589–600.
7. WEATHERLEY, P. E. 1973. Solution flow in tubular semipermeable membranes. Planta 110: 183–187.
8. YOUNG, J. H., R. F. EVERT, AND W. ESCHRICH. 1973. On the volume flow mechanism of phloem transport. Planta 113: 355–366.