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Unidirectional Movement of Tracers along the Stolon of Saxifraga sarmentosa

F. A. Qureshi and D. C. Spanner
Bedford College, London

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Summary. When radioactive tracer is applied locally to the stolon of Saxifraga its long-distance movement after 18 hours is found to be strongly polarised; there is in addition a short-distance movement which is unpolarised. With caesium, the long-distance movement is predominantly in the phloem; with strontium in the xylem. These interpretations, a priori probable, were confirmed by artificially reversing, separately, the xylem and the phloem currents. With long pieces of excised stolon only the unpolarised short-distance movement is observed. These results constitute evidence against simultaneous bidirectional translocation in the same sieve tube, and are consistent with either the Münch or the electro-osmotic theory.

Introduction

The possibility that phloem tissue can conduct simultaneously in both directions is one which early attracted attention, for not only is it of interest in connection with the recognised requirement for different solutes to move concurrently upwards and downwards (e.g. mineral ions and assimilates respectively); it has also an obvious bearing on the intriguing question of sieve tube transport mechanism. In so far as such bidirectional conduction is shown to be a property of the axis as a whole the point is not crucial for mechanism; it is when the evidence is narrowed down to the single sieve tube that it becomes decisive. This is because the various hypotheses are rather sharply divided on this issue; some, such as the “transcellular strand” theory (Thaine, 1964) and perhaps “activated diffusion”, can readily accommodate it, while the mass-flow theories fairly obviously cannot. In the latter category are the pressure-flow theory of Münch, and the potassium or electro-osmotic theory. These two hopeful hypotheses would therefore be excluded if unimpeachable evidence were forthcoming that individual sieve tubes could conduct simultaneously in both directions. Evidence which prima facie appears such has recently been provided (Eschrich, 1967; Trip and Gorham, 1968), and Trip and Gorham have in fact reached the firm conclusion that “bidirectional movement of sugars in the same sieve tube has been observed. ... The mass flow theory ... is no longer adequate to explain these observations.” However, Peterson
and Currier (1969) in a paper providing a very useful critique of the historical evidence have given an alternative interpretation of Trip and Gorham’s results, an interpretation which the present authors feel does real justice to the situation. In fact, the data given by Trip and Gorham possibly justify it to a rather greater extent than Peterson and Currier have remarked. For in their Fig. 1 (Trip and Gorham, 1968) the authors have noted the $^{14}$C count at two points on the petiole below the $^{14}$C-fed leaf. If the usual exponential fall-off relationship holds for this petiole and for the stem below it then at the point of junction with the older petiole conveying tritiated sugar there would be a $^{14}$C count of possibly 500–1000. Thus if there are sieve tubes carrying tritiated sugar into the $^{14}$C-fed leaf from this point, then clearly these tubes could become labelled with $^{14}$C at this node. This would seem to be a quite credible point of view, and until it is successfully disputed Trip and Gorham’s dismissal of a mass-flow mechanism cannot be accepted. Peterson and Currier’s presentation of their own positive evidence to the contrary, i.e. in favour of unidirectional flow, seems difficult to gainsay.

The work reported in the present paper is in several respects complementary to that of Peterson and Currier. Whereas they used plant axes which $a$ priori would be expected to be conducting in both directions simultaneously, and showed that for short periods of translocation, bundles labelled with tracer above the reservoir did not carry it below, and vice-versa, we have used axes which $a$ priori would be expected to be conducting unidirectionally. This has meant that experiments could be run for much longer periods, there being no problem arising from lateral transfer at the nodes. To some extent therefore the results meet the objection noted by Peterson and Currier (and partly answered by them) that movement in one direction might be much slower than in the other. Secondly, whereas they used fluorescein as tracer we have used $^{137}$Cs, $^{85}$Sr and though it is not reported here, $^{14}$C-labelled sucrose. This, especially the fact that we have used labelled sucrose, reduces any uncertainty arising from the use of such a non-physiological substance as fluorescein. Finally, we have recorded not the presence or absence of tracer in the bundles, but its quantitative longitudinal distribution along the axis. This enables us to establish the quantitative difference between movement in the two directions, and to distinguish (in a less direct way than Peterson and Currier) between phloem and xylem transport.

**Materials and Methods**

The experiments to be described were performed on the stolons of *Saxifraga sarmentosa* (Fig. 1). The plants were grown in plastic pots in the greenhouse in the usual way, except that the stolons were allowed to hang vertically into a