







conflict with the results presented here is only apparent; his 'cambium' fractions in fact contained differentiating xylem and phloem tissue (Söding, 1940), and the xylem and phloem tissues he analysed were not differentiating but mature. Furthermore, the auxin was not extracted but collected by diffusion methods of dubious reliability for comparing different tissues. Söding admitted the possibility that the auxin might be present in differentiating vascular tissue, but rejected it as being 'plainly improbable'. ("Außer der handgreiflich unwahrscheinlichen Annahme, daß nicht das Kambium, wohl aber das jüngste Holz und die jüngste Rinde wuchsstoffhaltig seien, bleibt also nur der Schluß, daß das Kambium selbst ein Hauptsitz des Wuchsstoffes ist" (Söding, 1940, p. 133).) He had previously (Söding, 1937) pointed out that except in coleoptile tips, auxin is in general formed in meristematic and growing regions, and implied that it is made by the meristematic or growing cells themselves. There is as yet no direct evidence that auxin is produced by meristematic cells. There is, on the other hand, evidence that auxin is formed by autolysing cells and that in higher plants it is normally produced as a consequence of cell death (Sheldrake and Northcote, 1968*a, b, c*). The high levels of auxin associated with developing embryos could be produced as the nutritive tissues surrounding them regress and die, and the production of auxin in other areas of meristematic activity could be explained by the association of meristematic activity with vascular differentiation; the differentiation of xylem cells involves their death. In contrast to Söding's expectations, this hypothesis predicts that higher amounts of auxin should be detected in differentiating xylem tissue than in the cambium. The auxin found in the xylem cannot be ascribed to its presence in xylem sap travelling within mature xylem vessels since the xylem sap of trees contains practically no auxin (Sheldrake and Northcote, 1968*d*). So unless there is an unlikely lateral transport system for auxin against a concentration gradient, the results reported in this paper strongly suggest that auxin is formed in differentiating xylem cells, and support the dying-cell hypothesis of auxin production.

The reactivation of the cambium in the spring is known to depend on the presence of expanding buds, which are rich in auxin, or if these are removed, on a supply of exogenous auxin (Reinders-Gouwentak, 1965). This requirement for auxin does not imply that a supply of auxin from the shoots is necessary for the maintenance of cambial activity once it has been initiated. The auxin formed by the developing buds in the spring could have a 'priming' effect on the cambium. If in general auxin is produced as a consequence of cambial activity in quantities sufficient to stimulate further cambial activity, in the intact plant the subsequent control of the cambium must be brought about by factors other than the supply of auxin from the shoots and leaves. In many species cambial activity continues after shoot growth has ceased (Priestley, 1930; Wareing and Roberts, 1956). Wareing and Roberts (1956) found that the maintenance of cambial activity in *Robinia pseudacacia* depended on the exposure of the leaves to long days; they suggested that either mature leaves under long days produce a cambium stimulus, or that short-day treatments lead to the formation of an inhibitor of cambial activity. If stimulation rather than inhibition is involved,

auxin seems unlikely to be responsible since mature leaves produce little auxin and differences in auxin production by such leaves under long and short days have not been detected (Chailakhyan and Ždanova, 1938; Bonner and Liverman, 1953). In some diffuse porous trees cambial activity ceases with the termination of extension growth. Again the available evidence does not make it possible to decide whether the cessation of cambial activity is due to inhibition or to the lack of a stimulus which the mature leaves of the tree are presumably unable to provide. But even if an influence from leaves or shoots is necessary for the maintenance of cambial activity in some species, at least in the case of tobacco no such stimulus is required: in the absence of exogenous hormones cambial activity continues in excised internodes in sterile culture for many months (Sheldrake and Northcote, 1968a).

The gradient of auxin from xylem to phloem across the cambium means that cambial derivatives must be in different hormonal environments on different sides of the cambium. Moreover, on the phloem side the presence of mature, functional sieve elements is likely to mean that cells in lateral and longitudinal proximity to them are exposed to relatively high concentrations of sucrose and other translocated metabolites. Both sucrose and auxin are necessary for organized vascular differentiation; a high sucrose to auxin ratio leads to phloem differentiation, and other combinations of these two factors stimulate xylem differentiation (Wetmore and Rier, 1963; Jeffs and Northcote, 1967; Rier and Beslow, 1967), which in turn leads to further auxin production. This could help to explain how the cambium and its derivatives can form a stable pattern of differentiation which is self-catalysing and self-perpetuating (Sheldrake and Northcote, 1968a).

#### ACKNOWLEDGEMENTS

I thank Professor F. G. Young, F.R.S. for making research facilities available to me in the Department of Biochemistry. This work was carried out during the tenure of the Royal Society Rosenheim Research Fellowship.

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