no evidence of bud blast or leaf injury. The bloom period is 7 to 10 days after *R.* 'PJM'.

MODERATOR DIRR: Joe McDaniel has three plants to present.

JOE McDANIEL: *Maclura pomifera* 'Altamont' is the name of a thornless selection of osage orange that I have selected. The plant is a staminate form and has a more upright branching habit than is usual for the species.

Magnolia 'Spring Joy' is a cross between *M. kobus* var. *stellata* 'Royal Star' and *M.* 'Wada's Memory'. *M.* 'Spring Joy' has more tepals than *M.* 'Wada's Memory' and the flower opens later than *M.* 'Royal Star'. Its color is prevailingly white with a touch of pink at the base. *M.* 'Spring Joy' will mature larger than *M.* 'Royal Star' which is one of the more vigorous *M. kobus* var. *stellata* cultivars.

Magnolia 'Paul Cook' is the result of a cross between *M. sprengeri* and a seedling of *M.* × *soulangiana* 'Lennei'. This cultivar has been hardy through all the bad winters at Urbana, Illinois. It has light pink blooms, as much as 11 inches across, which are borne on stronger growing trees than *M.* × *soulangiana*.

BACK TO THE BASICS OF ROOTING

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The phenomenon which nurserymen call rooting is really a combination of several processes and chemical interactions, often separated into root initiation and root development. In the first, cells capable of rejuvenating and becoming meristematic, receive appropriate chemical signals and start dividing. In the second, these meristematic groups of cells called root initials respond to different sets of signals and continue division and elongation into young roots, aided by factors in the environment.

Physiologists ask the nature of the signals, which cells perceive them, and why root cells are produced and not some other type. These are important considerations, because the theory of totipotency suggests that all cells in plants have the

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genetic information to make a complete new plant.

First, what types of cells have the ability to rejuvenate, dedifferentiate or to divide again, and where are these cells located? Many cells are so differentiated that it is difficult if not impossible for them to divide again. As examples, the vessels in the xylem which carry water and nutrients upwards from the roots to the stems are thick-walled and are dead in most respects, and thus are not able to divide. Similarly, sieve tubes in the phloem which carry sugars and hormones and other substances usually downwards from the leaves to the roots do not become meristematic again, and thick-walled cells such as fibers are not likely candidates for division. Instead the parenchyma cells, large blocky cells found throughout plants in many tissues, can revert to meristematic activity very easily, and it is generally the parenchyma cells which start division to form root initials.

Location is another interesting question. Why don't all of the parenchyma cells in a stem become meristematic and produce roots? Usually, in stems parenchyma cells near or just outside the phloem, in phloem rays, or in the interfascicular region between vascular bundles most often produce root initials. In roots, secondary roots usually develop from the pericycle area, just outside the phloem. Although other cells can produce roots, particularly those in tissue cultures, in intact plants parenchyma near the phloem tissue is most likely.

Interestingly, the vascular cambium which is responsible for the formation of most other cells in plants usually does not produce root initials, even though these cells apparently have the information to do so.

A basic scheme for root initiation and development (Fig. 1) was prepared many years ago (2) and is still not worked out completely. The first step was the identification of indoleacetic acid in 1934. IAA, produced in developing buds, young leaves, root tips, pollen, and fruits, was the first natural growth regulator in plants to be identified. Within months of its identification, IAA was added to cuttings to promote formation of root initials, although other compounds such as indolebutyric acid (IBA) and naphthaleneacetic acid (NAA) were found to be of greater commercial use because of stability and mobility. The movement of IAA downward in a stem from the young buds and accumulating at the base of a cutting, or addition of IBA at the base of the cutting, is one signal for root initiation.

However, it has been known for many years that there are growth regulating compounds other than auxins which are necessary for root initiation. The work of van der Lek (9), Went (10), and others pointed toward the existence of such compounds, and the term "rhizocaline" was coined for such unknown substance(s). The work of Hess (5) and students made some of the first separations of root promoting substances other than auxins, named cofactors 1, 2, 3 and 4, and later found in many plants. The levels and balance of these 4 cofactors were used to explain differences in rooting in juvenile and adult ivy, and among rhododendron cultivars (6).

However, an increasing amount of evidence suggested that levels of cofactors and auxins do not always correlate well with rooting, as in explaining differences in rootability among chrysanthemum cultivars (12), and bougainvillea, among others. These results lend support to the scheme in Fig. 1 which proposes that an enzyme is necessary to complex auxins and cofactors to provide the primary stimulus for root initiation. Despite some work, a single enzyme has never been isolated from a plant, which added to auxins and cofactors induces rooting. However, recent work just completed in England (1) has isolated a polyphenolic oxidase enzyme from apple cuttings, which when added in a crude preparation to apple cuttings, improves rootability at times when the cuttings would not normally root well. Although the enzyme has not been purified, and has not shown to be active in all plants, the research supports the idea that auxins, cofactors, and a complexing enzyme are all needed for root initiation, and without any of the three, rooting will not occur.

The work of Bassuk (1) and others (4) also suggests that there may be more than 4 cofactors in plants. In fact, there may be specific compounds in specific plants and even individual cultivars which may act as cofactors, such as phloridzin in apple. Many so called secondary metabolic products in plants have been shown to have a positive effect upon root initiation in a particular plant or group of plants, but when applied to a wide range, do not seem to be successful (7).

Therefore, the scheme first proposed by Bouillene and Bouillene-Walrand (2) 25 years ago is on the verge of being proved correct. Auxins are necessary, and in softwood cuttings which are producing large amounts of auxins, additional applications may be helpful but not necessary. However, in hardwood cuttings which are not growing and in which the levels of auxins may be lower, exogenous applications have been very useful. However, as any propagator knows, even large applications of auxins do not always produce roots.

Second, cofactors, which may be very specific for each plant, are also necessary for root initiation. Since most cofactors have never been identified conclusively, they are not added to cuttings commercially at the present time. Thus, taking cuttings at the right time or treating them with the correct environmental factors may influence the development of these cofactors. The use of externally applied cofactors may increase as more is learned of their specific role in initiation.

And third, an enzyme similar to that hypothesized to conjugate auxins and cofactors has been found in apple cuttings, and if this enzyme is universally found in plants, and if it is effective in other species, perhaps an important biochemical riddle of root initiation will be closer to being solved.

These results suggest some explanation of why roots develop near phloem tissue. Auxins and cofactors are translocated primarily in the phloem, so interruption of the phloem when taking a cutting will allow accumulation of these materials at the base of the cutting in the phloem or nearby cells. Perhaps the enzyme necessary for complexing auxin and cofactors may be located in the cells of the pericycle area adjacent to the phloem. If this is the case, then the combination of auxins, cofactors, and enzyme, would be present in one location, stimulating parenchyma cells nearby to rejuvenate and become root initials.

It is important to know precisely the effect of a chemical or treatment on rooting, because the same substance may have differing effects upon different stages of root production. For example, relatively high concentrations of auxin are necessary for root initiation, concentrations which are inhibitory to further root development. The gibberellins limit root development by stimulating competing growth, although they apparently have no direct effect upon initiation. Abscisic acid and certain other inhibitory substances such as B-Nine which, in some plants, promote rooting (8) do so by interfering with the depressing effects of gibberellins. Further, chemicals which seem to act as cofactors may instead have an indirect effect upon root initiation, as in the effect of catechol which protects IAA from destruction, thus improving root initiation (3,4). Mineral nutrients, which have been shown to aid rooting of herbaceous and softwood cuttings (11) have an influence upon root development, but little effect upon initiation.

Carbohydrates are important also in rootings. But as Figure 1 shows, the greatest effect of carbohydrates is in root development rather than root initiation. Since carbohydrates cannot be added to cuttings effectively, it is important to regulate sugar content in other ways. Hardwood cuttings already contain large amounts of stored sugars, and this explains why conservation of carbohydrates is so important, by such means as cooler temperatures and lower light intensity. In contrast, softwood and herbaceous cuttings do not have large amounts of stored carbohydrates and production during rooting is important. This explains why leaves are left attached and why warm temperatures and relatively high light intensities are preferred for softwood and herbaceous cuttings, as long as transpiration can be controlled, as by intermittent mist.

No longer is it sufficient to talk about "rooting." Instead effects of treatments must be associated with the specific processes which occur during root production and a more precise appreciation of the nature of these processes by plant propagators is necessary.

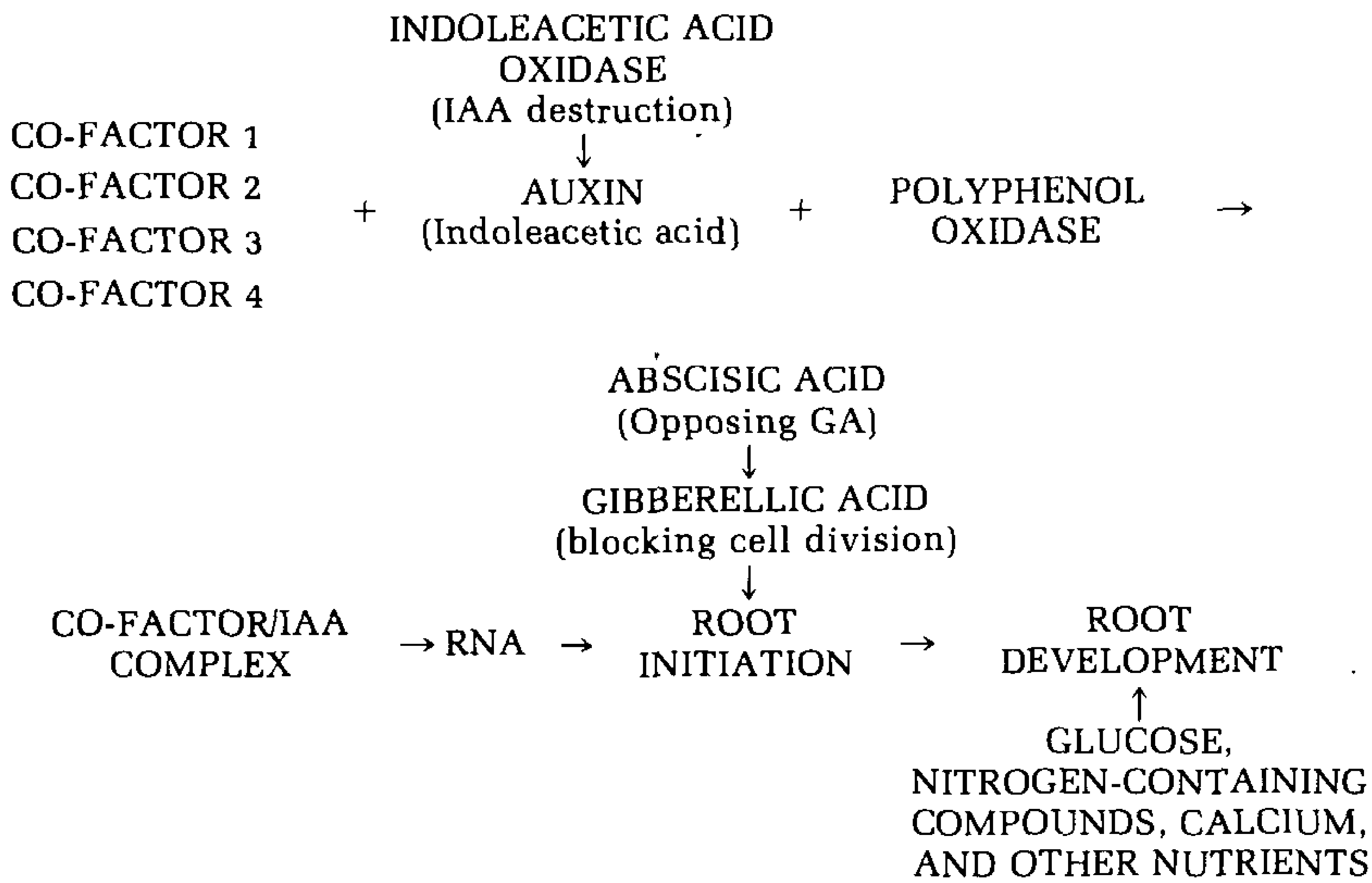

Figure 1. Scheme of root production (from 4).

LITERATURE CITED

1. Bassuk, N.L. 1980. Studies of seasonal changes in rooting of leafless woody apple cuttings. Ph.D Thesis, Univ. of London. UK.
2. Bouillenne, R. and M. Bouillenne-Walrand. 1955. Auxines et bouturage. *Rpt. 14th Inter. Hort. Cong.* 1:231-238.
3. Hackett, W.P. 1969. The influence of auxin, catechol and methanolic tissue extracts on root initiation in aseptically cultured shoot apices of the juvenile and adult forms of *Hedera helix*. *Proc. Inter. Plant Prop. Soc.* 19:57-68.
4. Hartmann, H.T. and D.E. Kester. 1975. *Plant propagation: Principles and Practices.* 3rd ed., Prentice Hall, Inc., Englewood Cliffs, NJ.
5. Hess, C.E. 1961. Characterization of rooting cofactors extracted from *Hedera helix* L. and *Hibiscus rosa-sinensis* L. *Proc. Inter. Plant Prop. Soc.* 11:51-57.
6. Lee, Choong 11. 1969. The relationship between rooting cofactors of easy and difficult-to-root cuttings of three clones of rhododendron. *Proc. Inter. Plant Prop. Soc.* 19:391-398.

7. ________ and H.B. Tukey, Jr. 1971. Development of root promoting substances in *Euonymus elatus* 'Compactus' under intermittent mist. *Proc. Inter. Plant Prop. Soc.* 21:343-351.

8. Read, P.E. 1968. The effect of B-nine and cycocel on the rooting of cuttings. *Proc. Inter. Plant Prop. Soc.* 18:312-318.

9. van der Lek, H.A.A. 1925. Root development in woody cuttings. *Meded. Landbouwhoogesch., Wageningen:* 38.

10. Went, F.W. 1929. On a substance causing root formation. *Proc. Kon. Ned. Akad. Wet.* 32:35-39.

11. Wott, J.W. and H.B. Tukey, Jr. 1965. Propagation of cuttings under nutrient mist. *Proc. Inter. Plant Prop. Soc.* 15:86-94.

12. Zondag, R.J. 1972. The levels of rooting cofactor 4 in *Chrysanthemum morifolium* during propagation. M.S. Thesis, Cornell Univ., Ithaca, NY.

JIM WELLS: I understood that the cambium was the seat of all adventitious formation.

HAROLD TUKEY: In general we do not get roots coming directly from cambial cells. Most root initials arise from cells near the cambium which are young and can dedifferentiate.

MICHAEL DIRR: How is a large macromolecule, such as a protein, getting into the root initial cells? It seems a little dubious to me.

HAROLD TUKEY: In the experiments reported from East Malling, they have taken the crude extract, applied it back to other plants, and it works. You would not expect large molecules to get into the cells but it does work. It has worked on apple and some other woody plants.

MICHAEL DIRR: How do they know it is the enzyme and not some other material?

HAROLD TUKEY: They can not prove that at this point. However, it has been purified of hormones, such as the auxins.