5. SOMATIC EMBRYOGENESIS IN WOODY PERENNIALS

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1. INTRODUCTION

1.1. Extent of this review

Since the first reported induction of somatic embryogenesis in carrot cell cultures more than 25 years ago (131, 151), there has been significant progress and numerous reviews (3-6, 8, 17, 25, 35, 40, 41, 48, 51, 98, 103, 123, 126, 128, 135, 145, 166, 167). Consequently, this review will emphasize the more recent work on woody perennials, including conifers and woody monocotyledonous plants. Reviewed elsewhere in this series are somatic embryogenesis in endosperm (Lakshmi Sita), haploids (Rohr, Chen), and the role of ammonia in somatic embryogenesis (Durzan).

1.2. Definition of terms

Somatic embryogenesis has been defined clearly by Haccius (46) as a non-sexual developmental process which produces a bipolar embryo from somatic tissue. Developmental stages similar to normal embryogenesis occur and yield an embryo with no vascular connection to the parent tissue. Sharp et al. (136) distinguished two types of somatic embryogenesis, direct and indirect. Direct somatic embryogenesis refers to the development of an embryo directly from the original explant tissue. Indirect somatic embryogenesis is the formation of embryos from callus or cell suspension, or from cells or groups of cells of somatic embryos. The latter process is called "repetitive somatic embryogenesis" (3, 4). Embryos derived in this manner are sometimes described as adventive or secondary. Embryos from tissues such as the megagametophyte of conifers would be formed by the process of gametophytic embryogenesis. Any cells which can develop into somatic embryos are said to possess embryogenic competence. Whether these cells are target...
cells which respond to special signals or whether most cells have this capability is not yet known. The selection of specific developmental stages of explant material, conditioning media, sequential transfers and appropriate environmental conditions are generally necessary for successful embryogenesis. The primary events required for cells to enter the developmental program of embryogenesis are unknown, but the techniques are available to begin to address this question.

1.3. Woody perennials

The introduction of somatic embryogenesis in woody perennials dates from the early work of LaRue (82) and research with Biota orientalis Engl. (69) and Zamia integrifolia Ait. (105). Somatic embryogenesis has since been induced in more than 25 families, 44 genera, 60 species and numerous cultivars of trees (Table 1). Among characteristics of woody plants which make them more intractable for studies of somatic embryogenesis are: 1) the short seasonal period of time when any particular tissue or stage of development is available for culture, 2) the long period required for regeneration, 3) the frequent production of phenolic compounds in browning reactions, and 4) the long term commitment required for productive research. A singular advantage, however, is the long life of the individual plant. The potential for propagating new germplasm from protoplast fusion products, embryogenic lines derived from wide crosses, somatic variants, and bioengineered creations might well be justified in forest crops (96) orchard trees or other woody species.

2. METHODS

2.1. Explant source

Initiating the developmental program for somatic embryogenesis from a cell or a group of cells frequently depends on the nature of the explant source. This refers to the conditions under which the source plant was grown and the stage of development of the plant part from which the explant was taken. Juvenile tissues of certain types appear to be the most suitable for induction of somatic embryogenesis. Mullins and Srinivasan (97), who first reported somatic embryogenesis from the nucellus of grape, refer-