

ORGANOGENESIS FROM INTERNODE-DERIVED NODULES OF *HUMULUS LUPULUS* VAR. NUGGET (CANNABINACEAE): HISTOLOGICAL STUDIES AND CHANGES IN THE STARCH CONTENT¹

ANA M. FORTES² AND MARIA S. PAIS

Centro de Biotecnologia Vegetal, Faculdade de Ciências, Univ. Lisboa, Bloco C2, Piso 1, Campo Grande, 1780 Lisboa, Portugal

The sequence of histological and histochemical events occurring during organogenesis from *Humulus lupulus* var. Nugget internode-derived nodules was studied. Sections were made and studies were carried out from the start of culture treatment until the development of shoot buds. Cell division was observed in both cambial and cortical regions during the first week of culture establishment. Cell division in cortical cells led to the formation of an incipient callus tissue. From the calluses prenodular structures of cambial origin appeared and gave rise to nodules from which shoot buds formed. Nodules kept separating into "daughter nodules" from which arose an increasing number of shoot buds. Iodide staining showed a strong starch accumulation in callus tissue and in prenodular structures. During shoot-bud primordia formation starch content decreased in nodules. Some starch was also noted in control explants (cultured on basal medium), however at a lower level than that observed in explants cultured on media with growth regulators. Shoot-bud regeneration was not observed in control explants.

Key words: Cannabinaceae; histological studies; *Humulus lupulus* var. Nugget; internodes; nodules; organogenesis; starch.

The totipotent character of plant cells and tissues can be expressed by their ability to regenerate into plants via embryogenesis or organogenesis. Both processes lead to in vitro regeneration and are a major prerequisite for genetic transformation. However, the widespread application of gene transfer techniques for crop improvement cannot be successfully achieved if the processes leading to morphogenesis are not well understood.

Histological, histochemical, and ultrastructural aspects of somatic embryogenesis, whether occurring with or without a callus phase, have been extensively reported (Ho and Vasil, 1983; Williams and Malleshwarum, 1986; Stamp, 1987; Pedroso and Pais, 1993; Brisibe et al., 1993; Sagare, Subasini, and Krishnamurthy, 1995). A system of efficient regeneration parallel to somatic embryogenesis has been recently proposed (Aitken-Christie, Singh, and Davies, 1988; McCown et al., 1988; Warrag, Lesney, and Rockwood, 1991; Teng, 1997) and is based on the formation of organogenic nodules that arise directly from the explants or from callus and cell suspension cultures.

Morphogenesis requires an external source of carbon, which is usually supplied in the medium mainly as sucrose. Thorpe and Murashige (1970) and Mangat, Pelekis, and Cassels (1990) have shown that in tobacco callus and in *Begonia rex* stem explants there is a strong accumulation of starch in areas that eventually give rise to meristemoids and shoot primordia in tissues grown on shoot-forming media. High amounts of starch have also

been observed during somatic embryogenesis in sugar cane and cassava (Ho and Vasil, 1983; Stamp, 1987). The possible role of starch in these processes is not clear. It has been suggested that starch may function as an energy source or may provide osmoticity in the form of free soluble sugars (Thorpe, 1980; Stamp, 1987). Regardless of its function, starch accumulation/mobilization cycles appear to be a characteristic feature of cells involved in plant morphogenesis.

This paper reports on the histological events leading to nodule formation and shoot regeneration from internode-derived nodules of *Humulus lupulus* var. Nugget and on the evidence of a starch accumulation/mobilization cycle during this morphogenic process.

MATERIALS AND METHODS

Tissue culture.—Internodal explants were taken from 3–4 mo old plants micropropagated in Adams (1975) media. Explants were first cut into pieces 6–9 mm long and then inoculated in culture flasks (9 × 8 cm) containing ~40 mL of MS solid medium (Murashige and Skoog, 1962) supplemented with 2 mg/L BAP, 0.05 mg/L IAA, 18 g/L sucrose, and 7.8 g/L agar (Vas Pereira, Lisbon, Portugal). Control explants were cultured as described above but on medium without growth regulators. The pH was adjusted to 5.7–5.8 before autoclaving at 121°C and 1.01 × 10⁵ Pa for 18 min. All cultures were incubated at 25° ± 2°C with a 16-h photoperiod (35 μmol photons·m⁻²·s⁻¹) provided by cool-white Philips fluorescent tubes.

Histology and histochemistry.—Cultured explants were removed at random at 0, 2, 5, 7, 9, 12, 15, 19, 23, 28, 31, 35, and 45 d and fixed in 30% formalin:glacial acetic acid:70% ethanol (1:1:18) for 72 h at 4°C. Control explants were removed after 8, 15, 28, and 45 d in culture on MS medium without growth regulators and fixed as described above. Sections (20–40 μm) of the fixed internodal segments were obtained

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² Author for correspondence (anforges@fc.ul.pt).

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web anatomy of the frog s mouth pry the frog s mouth open and use scissors to cut the angles of the frog s jaws open cut

deeply so that the frog's mouth opens wide enough to view the structures inside 1 locate the tongue play with the tongue does it attach to the front or the back of the mouth you may remove the tongue

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web when the abdominal cavity of the frog is opened many organs of the digestive and urogenital systems can be observed as you read the descriptions of the organs below color them on the diagram leading from the mouth is a tube that connects to the stomach color the esophagus pink

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fertilization hindlimbs aid in swimming climbing and jumping movement forelimbs aid in gripping surfaces during locomotion movement digits

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