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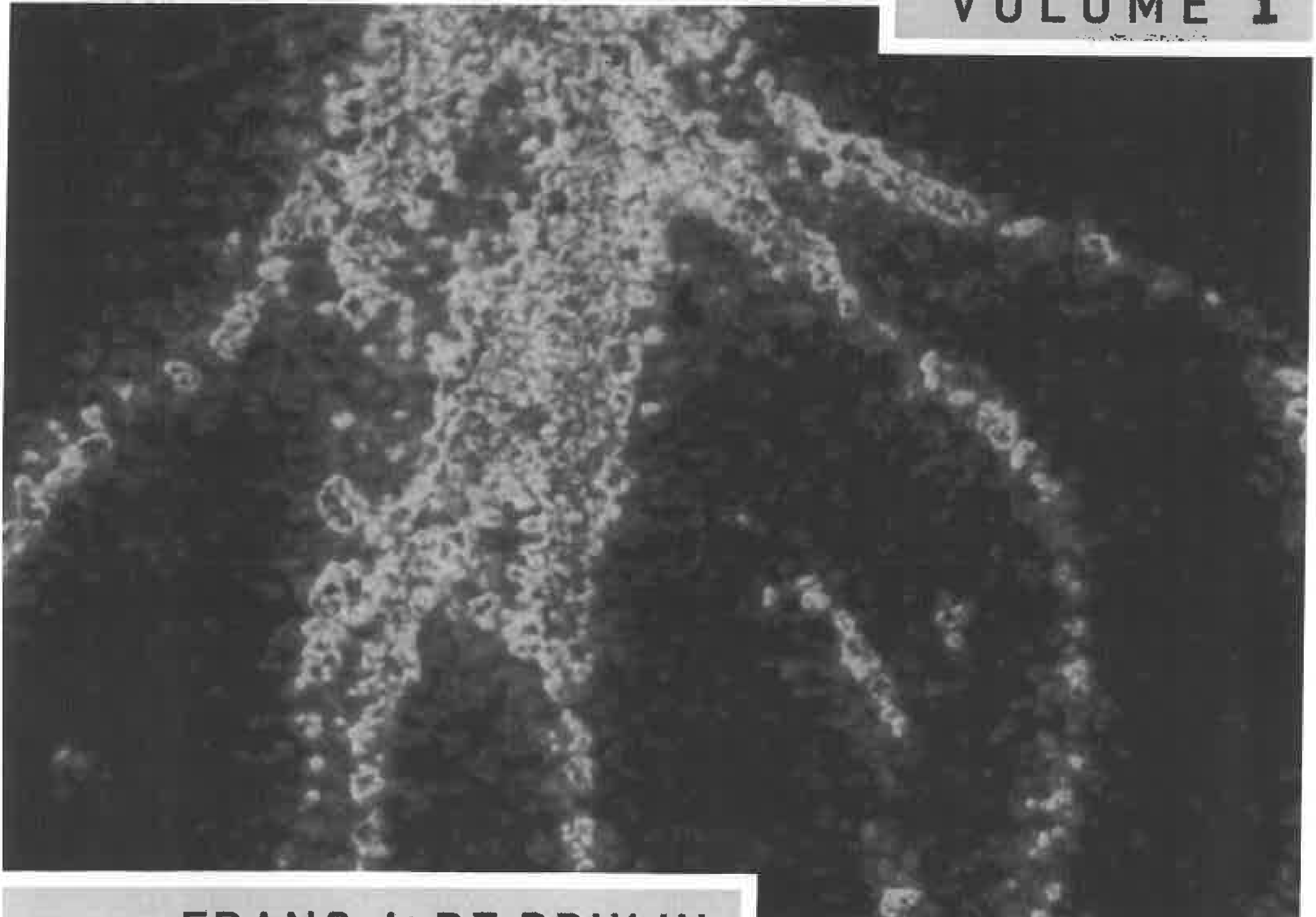

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Cover Photo: Bioluminescence image of a barley root system colonized by *Pseudomonas fluorescens* strain DF57-40E7 visualized by a Hamamatsu photonic camera system. Strain DF57-40E7 emits bioluminescence due to an inserted Tn5::*luxAB* gene cassette. Image courtesy of Lene Kragelund, Frans de Bruijn and Ole Nybroe.

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Chapter 51

Roles of Flavonoids in Symbiotic Root–Rhizosphere Interactions

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51.1 INTRODUCTION

51.1.1 Flavonoid Synthesis and Occurrence in Plants

Flavonoids are metabolites of the phenylpropanoid pathway, which are synthesized from *p*-coumaroyl-CoA and malonyl-CoA and share their precursors with the lignin biosynthetic pathway (Stafford, 1990). Flavonoids have been found in all plants, and so far over 10,000 flavonoids have been identified in different plant species (Ferrer et al., 2008). The diversity of flavonoids is achieved through the generation of several basic flavonoid structures, including flavonols, flavan-3-ols, flavones, flavanones, isoflavonoids, isoflavans, and pterocarpans (Fig. 51.1). A diversity of end products is derived from the modification of these basal structures, e.g. by glycosylation, methylation, hydroxylation, malonylation, acylation, prenylation, or polymerization (Winkel-Shirley, 2001). These modifications can alter the solubility, mobility, degradation, and function of flavonoids inside the plant and in the rhizosphere.

Flavonoid synthesis has been well studied, and the majority of enzymes have been identified (Dixon and Steele, 1999; Winkel-Shirley, 2001; Du et al., 2010). The synthesis of flavonoids starts on enzyme complexes that are located at the cytosolic side of the endoplasmic reticulum (Jorgensen et al., 2005). Flavonoid intermediates can subsequently be channeled into the vacuole for storage, often after being glycosylated by enzyme complexes located at the tonoplast (Aoki et al., 2000; Winkel, 2004). The accumulation of final flavonoid end products is often specific for particular cell types. In roots, flavonoids often accumulate at the root tip and in root cap cells. Flavonoid accumulation in specific cell types of the root, for example, in precursor cells of nodules, have been linked to specific functions in root development (Mathesius et al., 1998a; Mathesius, 2001). Intracellularly, flavonoids can be found in the cytoplasm, the vacuole, the nucleus, the cell wall, or in cell membranes (Hutzler et al., 1998; Erlejman et al., 2004; Saslowsky et al., 2005; Naoumkina and Dixon, 2008). Several transcription factors, in particular, those of the MYB and bHLH families, control the localization and synthesis of flavonoids in different tissues and in response to the environment (Koes et al., 2005). However, in most cases, the regulation of cell specificity remains unknown.

Despite the cell specificity of flavonoid synthesis, there is also evidence that flavonoids can be transported within and between cells and tissues. Flavonoids are thought to move via vesicle-mediated transport or membrane-bound transporters of MATE (multidrug and toxic extrusion compound) or ABC (ATP-binding cassette) families within cells (Zhao and Dixon, 2009). Transport of flavonoids between cells over long distances is less well understood. In *Arabidopsis*, it was demonstrated that external application of flavonoids led to their transport toward distal tissues (Buer et al., 2007). This mode of transport is most likely mediated by

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