7.1 Introduction

Cellulose biosynthesis inhibitor (CBI) herbicides are a small group of chemically unrelated compounds including the herbicides dichlobenil, isoxaben and flupoxam (Sabba and Vaughn 1999; Fig. 1). In addition, the auxinic-type herbicide quinclorac may have a second site of action in monocots that affects cellulose biosynthesis (Koo et al. 1996, 1997). Although they are a rather small group of compounds in relation to all of the herbicides, they have several qualities that make them quite important. For example, the lack of field resistance to these compounds and a site of action not shared by mammals make them an important group in terms of resistance management and approval by government agencies concerned with toxicological issues. Moreover, they appear to be useful tools to unravel the complexities of the plant cell wall and, more specifically, the production of cellulose.

CBI herbicides induce the same sort of symptomatology as the mitotic disrupter herbicides: swollen root tips after growth of the seedlings in the presence of the herbicide (Roberts 1990; Heim et al. 1998; Sabba and Vaughn 1999), so-called radial root swelling (Baskin et al. 1992). Because many assume that this symptom is associated only with mitotic disrupter herbicides, this single symptom may be misinterpreted, resulting in classification of the herbicide in the wrong group. Such was the case with flupoxam, a herbicide that induces extensive radial swelling of the root tips (O’Keefe and Klevorn 1991). However, subsequent investigations have not indicated any mitotic or microtubule effect of this herbicide (Hoffman and Vaughn 1996), yet substantial effects are noted on new cell wall synthesis (Heim et al. 1998; Vaughn and Turley 2001). Thus, although mitotic disrupter herbicides have been described classically as causing this effect, a herbicide should certainly not be placed in this group without further verification.

Another important distinction between CBI and mitotic disrupter herbicides lies in the selectivity differences of these groups. Mitotic disrupter herbicides are most effective on small seeded monocots (Vaughn 2000). The CBI herbicides are most effective on dicots, with either less dichlobenil (DCB) or no (isoxaben) effects on the monocots (Sabba and Vaughn 1999). Recently, Heim et al. (1998) have described subtle differences in root appearance that
Fig. 1. Chemical structures of the three major cellulose biosynthesis inhibitor herbicides: dichlobenil (right), isoxaben (center) and flupoxam (right)

might be useful in diagnosis of CBI symptomatology compared with mitotic disrupter herbicides.

7.2 Mode of Action Studies

Each of the CBI herbicides has been shown to inhibit the incorporation of radiolabeled glucose into an acid insoluble product that is assumed to be cellulose (Hogetsu et al. 1974; Heim et al. 1990a,b, 1998). Even though cellulose is the most abundant biopolymer in the world, attempts to obtain consistent cellulose synthase activity in vitro have been very difficult (see reviews in Delmer and Amor 1995; Brown et al. 1996). Instead, callose is often produced in these in vitro assays with a limited amount of cellulose. This makes such in vitro assay systems relatively useless in studying effects of these herbicides. Thus, certain in vivo systems that allow one to study de novo formation of cell walls or cellulose have been utilized to investigate CBI herbicides.

7.2.1 Cell Plates

Cell plates, which are cell walls formed to separate the daughter nuclei after cell division, are an attractive system for studying wall biosynthesis in that the wall is formed de novo in about 20–90 min, depending upon the species (Samuels et al. 1995). Moreover, recent advances in cell synchronization and cell plate ontogenesis have improved our understanding of how the various polysaccharides are assembled into this new wall (Samuels et al. 1995). These data indicate a prominent role of callose in causing cell plate spreading, whereas cellulose plays a role later in the development associated with cell plate stiffening.

DCB has been the most intensively studied in terms of cell plate formation. In the numerous light and electron microscopic studies, a consistent observation has been that the plates have been much more undulated and thicker than noted in the untreated cell plates (Fig. 2; Gonzalez-Reyes et al. 1986; Mineyuki