

DISCUSSION

Plants respond to infection by producing physical and chemical barriers which function as wall reinforcements, antibiotics or lytic enzymes. In every detailed comparative study of these responses, differences between resistance and susceptibility are quantitative rather than qualitative. Although susceptible plant possesses the machinery necessary for resistance, it is not activated in sufficient magnitude or speed to restrict infection (Kuc, 1983).

In the present investigation, at the onset, pathogenicity test of F.graminearum was carried out on ten soybean cultivars. Among the tested cultivars, Soymax was found to be highly susceptible while cv. UPSM-19 was found to be resistant. Phytotoxic effect of metabolic byproducts in the culture filtrate of F.graminearum on cvs. Soymax and JS-2 could be noticed. As soybean cultivars showed differential resistance to F.graminearum, it was considered worthwhile to detect the level of phytoalexin (glyceollin) accumulation in those cultivars in response to fungal infection which appeared to be the most promising line of approach in the study of disease resistance mechanism.

The majority of studies of resistance and susceptibility in soybeans to Phytophthora megasperma f.sp. glycinea have dealt with infections of the roots and hypocotyl region. This system has attracted attention also because it has provided a model system for study of the production and role of a phytoalexin (glyceollin) in a presumed gene-for-gene system (Yoshikawa et.al., 1978; Hahn et.al., 1985; Bhattacharyya and Ward, 1987). In another study it has been confirmed that resistant and susceptible responses can also be differentiated in leaves. However, responses of leaves were found to be greatly influenced by age and stage of development. Although Rps-gene-mediated cultivar resistance

was expressed, this was effective for a relatively short period in the development of leaves. All leaves became resistant as they aged, and very young unfolding trifoliolate leaves were susceptible even in resistant cultivars. Glyceollin accumulation in leaves was associated with the development of both Rps-gene-mediated and age related resistance (Ward, 1989).

Evidence that glyceollin, the pterocarpon phytoalexin from soybeans, occurs in several isomeric forms was provided by Keen et.al. (1971) for preparations obtained from soybean hypocotyls inoculated with the pathogen Phytophthora megasperma f.sp. glycinea. Subsequently the structures of four isomers (glyceollin-I-IV) were established by Burden and Bailey (1975) and Lyne et.al. (1976). Of these, glyceollin-IV has been isolated in minor amounts only, from cotyledons treated with CuCl_2 and no evidence that it may play a significant role in the resistance response has been provided. Glyceollins-I-III are all inhibitory to mycelial growth and zoospore germination of P.megasperma f.sp. glycinea and have been demonstrated to accumulate in significant amount in soybean tissues (Lyne et.al., 1976 ; Kaplan et.al., 1980; Moesta and Grisebach, 1981 ; Ingham, 1982; Hahn et.al., 1985 and Bhattacharyya and Ward, 1985). The proportions of the three isomers reported by different authors have varied considerably . Glyceollin-I predominated in roots treated with CuSO_4 (Morandi et.al., 1984) or inoculated with P.megasperma f.sp. glycinea (Hahn et.al., 1985) or hypocotyl treated with AgNO_3 (Stossel and Magnalato, 1983). In cotyledons, glyceollin -I and III have been reported to occur in roughly equal amounts following treatment with CuCl_2 (Lyne et.al., 1976). In leaves infiltrated with bacteria or sodium iodoacetate glyceollin-III was reported to be the main constituent. Although these reports suggest that there are major differences in the ability of soybean organs to synthesize the

three isomers, the possibility remains that the differences result from a combination of different experimental conditions and the use of different eliciting agents. None of these studies has examined the relationship of the accumulation of the three isomers to resistance and susceptibility in the host-pathogen interaction.

The results of present investigation revealed that resistant cultivars (cvs. UPSM-19, EC-55865 and R-184) contained more glyceollin than the susceptible cultivars (Soymax, JS-2 and KU-254). Present results substantiate the findings of previous workers who have also presented conclusive evidence that resistant cultivars of different host species produces more phytoalexins in response to fungal infection than the susceptible ones (Gray and Klarman, 1967; Klarman, 1968; Keen et.al., 1971; Keen and Horsch, 1972; Tjamos and Smith, 1974; Johnson et.al., 1976; Keen and Littlefield, 1979 ; Fraile et.al., 1980; Obi et.al., 1980; Purkayastha et.al., 1983; Rouxel et.al., 1989).

According to Keen(1971) the speed with which a plant produces phytoalexin may be of utmost importance if fungal colonization is to be halted at an early stage. The fungitoxic phytoalexin (glyceollin-I) accumulated in soybean hypocotyls of Harasoy-63 (resistant cv.), more rapidly (20-50 times faster) than in Harasoy (Susceptible cv.) after Challenge inoculation with Phytophthora megasperma var. sojae. Another interesting observation was made by Tjamos and Smith(1974) who showed that the rate of phytoalexin (rishitin) accumulation was relatively low in both Verticillium infected resistant and susceptible tomato cultivars during the first 2 days after inoculation but increased sharply after third day in resistant cultivar. In the present study glyceollin accumulation increased sharply after 48h of inoculation with F.graminearum in the resistant cultivars.

Partridge and Keen (1976) stated that Kievitone (Phytoalexin) was produced more rapidly in resistant cowpea plants than in near isogenic susceptible plants. They suggested that the rate of production of Kievitone was the basis for resistance of cowpea plants to Phytophthora vignae. Significant difference in phytoalexin (B-vulgarin) level in Cercospora beticola infected resistant and susceptible cultivars of sugar beet was also noted by Johnson et.al. (1976). When bean plants were inoculated with Botrytis cinerea, the amount of phytoalexin (Phaseollin) accumulation was always higher in partially resistant cultivar than in the susceptible one. Nemistothy and Guest (1990) have shown that a resistant and susceptible cultivar of tobacco differ in the magnitude and timing of phytoalexin, phenylalanine ammonia lyase activity and ethylene responses following infection by Phytophthora nicotine var. nicotianae. Each of these responses began earlier and proceeded at a faster rate in the resistant cultivar.

The aforesaid statements indicate that phytoalexin has a role in disease resistance in plants. The differential response of susceptible and resistant soybean cultivars to F.graminearum could probably be attributed to their capacity to accumulate more glyceollin. It seemed highly interesting, therefore, to induce changes in disease reactions by the application of certain chemicals capable of inducing phytoalexin production (Bell, 1967; Cheema and Haard, 1978 ; Purkayastha et.al., 1983; Sinha, 1984; Chakraborty and Purkayastha, 1987 ; Rouxel et.al. 1989) and to find out whether these changes could be correlated with enhanced glyceollin production.

A series of experiments have been performed using 12 chemicals belonging to 3 separate groups viz. 6 metal salts (Barium chloride, Ferric chloride, Cupric chloride, Cadmium

chloride, Mercuric chloride and Silver nitrate), 2 reducing agents (Sodium selenite and Sodium sulphite) and 4 metabolic inhibitors (Sodium fluoride, Sodium molybdate, Sodium azide and Sodium malonate) with a view to alter disease reaction in susceptible soybean plants (cv. Soymax). Apart from this, the effect of different concentrations of the above chemicals on spore germination of F.graminearum as well as effect of some selected chemicals on the mycelial growth of F.graminearum were also studied. Among the tested chemicals sodium azide, sodium selenite and sodium sulphite were found to be highly effective in reducing disease intensity. Moderate effect of sodium molybdate, cupric chloride and ferric chloride were also noticed on the alteration of disease reaction. However, no correlation could be drawn between germination percentage and rate of growth of the pathogen in vitro and in vivo experiments using those chemicals.

The use of nickel chloride as foliar spray to tea plants for the control of blister blight caused by Exobasidium vexans was demonstrated by Venkataram (1961). Host sensitization as a factor in induction of resistance in rice (cv. Dharial) against Drechslera oryzae by seed treatment with phytoalexin inducers have been reported by Sinha and Hait (1982). Among the 8 chemicals tested, all produced appreciable effects ; sodium selenite, lithium sulphate, cycloheximide, cysteine and thioglycolic acid caused marked reduction in symptoms in rice seedlings when challenge inoculated at the age of 3-4 weeks. With sodium selenite and thioglycolic acid induced effect persisted upto 8 weeks after sowing. Seed treatment of wheat with dilute concentrations of nickel chloride and barium sulphate significantly induced resistance to Drechslera sorokiniana (Chakraborty and Sinha, 1984). Protection of wheat seedlings against Helminthosporium sativum by seed treatment with chemicals (known to induce phytoalexin production in other plants) was also recorded by Hait and Sinha (1986). Sodium azide was also found to be most effective

in reducing charcoal rot disease of soybean caused by Macrophomina phaseolina (Chakraborty and Purkayastha, 1987).

All the above reports as well as the results of the present study, therefore, point to the ability of certain chemicals to induce protection, which in some cases, could be due to the direct fungitoxic effects of these chemicals on the pathogen, or it could be due to the activation of certain metabolic processes within the host cells leading to the production of greater amounts of antifungal compounds (phytoalexins). Reduction in disease symptoms after the treatment either with sodium azide or sodium selenite may be due to higher accumulation of glyceollin in treated plants (vide part VI). Results revealed that treatment with sodium azide induced a high level of glyceollin (545 $\mu\text{g/g}$ fresh wt.) after challenge inoculation with the pathogen in comparison to the untreated inoculated plants (256 $\mu\text{g/g}$ fresh wt.).

Several previous workers have also reported that certain chemicals are capable of inducing the production of antifungal compounds. It was reported by Keen et.al., (1981) that sodium iodoacetate acts as an abiotic elicitor of glyceollin in primary leaves of cv. Harosoy soybeans and that it is associated with the resistance expression. Copper sulphate, sodium nitrate and chloram-phenicol were found to be effective in inducing capsidiol production in Capsicum annum (Watson and Brooks, 1984). Accumulation of increased levels of glyceollin following treatment with sodium azide was reported by Chakraborty and Purkayastha (1987). Rouxel et.al., (1989) reported the accumulation of phytoalexin in CuCl_2 and AgNO_3 treated leaves of Brassica juncea.

The genetic information contained in nucleic acid is expressed in the cell via protein synthesis. Several proteins

function as enzymes in the metabolic pathways which synthesize or break down cellular components. When plants are infected by pathogens, the proteins in the penetrated plant cells are changed chemically and physically. Some enzymatic proteins are also produced in penetrated cells by pathogens themselves. Thus, qualitative and quantitative changes of proteins are related to both plants and pathogens (Uritani, 1971).

In the present investigation, it was noticed that protein content increased in the infected roots of susceptible cultivars (JS-2, PK-327 and Soymax). Increased protein level was also detected after infection of susceptible bean leaves by Uromyces phaseoli. Similar findings were reported by other workers (Tomiyama, 1966; Daly-1972; Ouchi et.al., 1974). They suggested that protein configuration changes in the host may induce the hosts' accessibility to the pathogen which is related to susceptibility. The greater accumulation of protein in susceptible host after infection could be attributed to the total proteins of both host and parasite. However, it is difficult to separate the relative contribution of host and parasite to the total protein content. Sometimes protein content of the host after inoculation remains unchanged but their isozyme pattern may change. Changes in protein patterns in barley leaves after inoculation with Erysiphe graminis f.sp. hordei could be detected by polyacrylamide gel electrophoresis (PAGE) study but there was no change in protein content of mildew infected barley leaves in comparison with healthy leaves (Johnson et.al., 1976). In the present study, protein patterns of healthy and F.graminearum infected soybean roots of susceptible (Soymax and JS-2) and resistant (UPSM-19 & PK-327) cultivars of soybean were evaluated by polyacrylamide gel electrophoresis. In healthy roots of cvs.Soymax and JS-2, 14 and 15 protein bands were detected while 16 and 18 protein bands in infected roots of cvs.Soymax and JS-2 respectively could be detected. On the other hand, both healthy and infected roots of cvs.UPSM-19 and PK-327 exhibited 15 &

17 protein bands. Mycelial protein of two isolates of F.graminearum, Fg1 and Fg2 exhibited 18 and 15 protein bands respectively. Changes in protein pattern of susceptible cultivars (Soymax and JS-2) after inoculation with F.graminearum as determined by PAGE cannot be compared with the protein bands of F.graminearum because proteins of dissimilar molecular weight may be observed in the same RF by this method. The present study atleast indicates the differences in protein patterns of isolate of pathogen as well as resistant and susceptible soybean cultivars before and after inoculation with F. graminearum.

Root protein of susceptible soybean cultivars inoculated with F.graminearum exhibited 2-3 additional protein bands, in relation to their healthy control. This is in conformity with the work of Uritani and Stahmann (1961) who reported that sweet potato infected by Ceratocystis fimbriata developed new proteins both in resistant and susceptible varieties. Five new isozyme bands such as acetyl esterase, acid phosphatase, malate dehydrogenase, succinate dehydrogenase and peroxidase were detected in the susceptible line of barley after inoculation with Erysiphe graminis f.sp. hordei (Sako and Stahmann - 1972). Differential changes in soluble leaf protein of tomato after inoculation with virulent and avirulent races of Cladosporium fulvum were determined by Dewit and Bakker (1980).

The presence of cross-reactive antigen (CRA) between plant host and their parasites and the concept that these antigens might be involved in determining the degree of compatibility in such interactions have been reviewed by several authors (De Vay et.al., 1972 ; DeVay and Adler, 1976; Kalyansundaram, 1978 ; Chakraborty, 1988 ; Purkayastha, 1989 ; Purkayastha et.al., 1991). In the present study root antigens of 3 cultivars each of resistant (UPSM-19, EC-55865 and R-184) and susceptible (Soymax, JS-2 and KU-254) soybean plants and

two isolates of F.graminearum (Fg1 and Fg2) were cross reacted separately with antisera of cvs. Soymax and UPSM-19. Reciprocal cross reaction was also carried out with antisera of isolate Fg1 and antigens of both susceptible and resistant varieties. Antigens from two non pathogens of soybean, viz. Glomerella cingulata and Pestalotiopsis theae were also considered for serological comparisons. It is significant to note that in immunodiffusion test susceptible cultivars (Soymax, JS-2 and KU-254) shared the common antigens with both the isolates of F.graminearum (Fg1 and Fg2) tested. However, antigenic disparity was noticed in cross-reaction and reciprocal cross-reaction with antigens and antisera of resistant cultivars and the isolates of the pathogen. Weak precipitin band was observed in cross reactions of antiserum of resistant cv. UPSM-19 with antigens of isolate Fg1 while no such precipitation could be detected with antigens of isolate Fg2 and antiserum of cv. UPSM-19. In reciprocal cross reaction with antiserum of F.graminearum (isolate Fg1) and antigens of resistant cultivars, precipitation bands could not be detected in cvs. UPSM-19 and EC-55865 but cv. R-184 developed weak precipitin band. Antisera of soybean cultivars and antigens of non pathogens (G.cingulata and P.theae) failed to develop any precipitin band.

Several earlier studies have also implicated the importance of common antigens in host-pathogen compatibility. Presence of CRA has been demonstrated in various host-parasite combinations such as flax and Melampsora lini (Doubly et.al., 1960), cotton and Verticillium albo-atrum (Charudattan and DeVay, 1972), cotton and Fusarium Oxysporum f.sp. vasinfectum (Charudattan & DeVay, 1970 ; Kalyansundaram et.al., 1975), sweet potato and Ceratocystis fimbriata (DeVay et.al., 1967), potato and Phytophthora infestans (Palmerley and Callow, 1978, Alba and DeVay, 1985), soybean and Macrophomina phaseolina (Chakraborty & Purkayastha, 1983), soybean and Colletotrichum

dematium var. truncata (Purkayastha and Banerjee, 1986), soybean and Myrothecium roridum (Ghosh and Purkayastha, 1990), jute and Colletotrichum corchori (Bhattacharyya and Purkayastha, 1985) Coffee and Hemileà vastatrix (Alba et.al., 1983), ground nut and Macrophomina Phaseolina (Purkayastha and Ghosal, 1987), Carrot and Pythium violae and Pythium sulcatum (Lyons and White, 1992) ground nut and Sclerotium rolfsii (Purkayastha & Pradhan, 1994), tea and Bipolaris carbonum (Chakraborty and Saha, 1994). Present result also support the findings of previous workers.

Conventional serological techniques have sometimes failed to detect cross reactive antigens in some host-parasite interactions such as wheat and Puccinia graminis var. tritici (Johnson, 1962), alfalfa and Corynebacterium insidiosum (Caroll et.al., 1972). The preparation and treatment of antigens are most important because most antigens are labile and easily denatured. The selection of test animal as well as the amount of antigen for immunization purpose are also important since too much material may reduce antibody formation. Moreover, a number of factors such as age of plant tissue, culture of microbes and methods of extraction of antigen have profound influence on the yield of antigenic substance and this may account for the failure to detect common antigens as suggested by DeVay and Adler (1976).

Alba et.al. (1983) showed that urediniospores of Hemileà vastatrix shared common antigenic determinant with coffee plant, in contrast to their previous conclusions made with the same host-parasite system (Alba et.al., 1973). This agreement was attributed to the low concentrations of antigenic preparations used in the earlier investigation.

Immuno-electrophoretic analysis with antigen and antisera preparation from soybean roots and F.graminearum also

substantiated the results of immunodiffusion tests. When antiserum of F.graminearum reacted with its own antigen, 6 precipitation arcs were formed of which 3 were common with cv. Soymax and 2 were common with cv. JS-2, KU-254 and R-184. No such precipitin arc was formed between antisera of F.graminearum and antigen of cv. UPSM-19 and EC-55865. However, in reciprocal cross reactions with antiserum of cv. UPSM-19 and antigen of isolate Fg1 one common precipitin arc was formed. No common antigenic relationship between host (Glycine max) and non pathogens was noticed. The present results are in agreement with the findings of Chakraborty and Purkayastha (1983), Purkayastha and Ghosal (1987). Purkayastha and his co-workers have examined various host-pathogen/non-pathogen combinations including cultivars of soybean, rice, jute, pigeon pea, bean, ground nut to find out their serological relationship with some fungal pathogens as well as non pathogens following agar-gel double diffusion and immuno-electrophoretic tests. More than 50% combinations exhibited cross-reactive antigen (CRA) between host and pathogens. No such CRA could be detected between resistant host and their respective pathogens. However, at a very low concentration CRA was detected between resistant host (soybean) and Colletotrichum dematium following enzyme linked immunosorbent assay (Purkayastha & Banerjee, 1990).

Enzyme linked immunosorbent assay has proved to be one of the most sensitive serological technique in detecting CRA at very low concentration (Alba & DeVay, 1985 ; Mohan, 1988 ; Chakraborty & Saha, 1994). In the present study the presence of CRA among F.graminearum and soybean cultivars was evident in indirect ELISA using antigen and antisera of host and parasite and goat antirabbit IgG conjugate. Indirect ELISA readily detected CRA in semipurified mycelial preparation at concentrations ranging from 5-25 μ g protein/ml with antiserum dilution of 1/125 and 1/250. Antigenic preparation (25 μ g/ml)

from F.graminearum (isolate Fg1) exhibited higher absorbance value at 405 nm with antiserum of susceptible soybean cultivar (Soymax) than the reaction with antiserum of resistant cultivar (UPSM-19). Higher absorbance value was also noticed in the reciprocal cross-reactions involving antiserum of the pathogen (isolate Fg1) and antigenic preparation of cv. Soymax (25 µg/ml) than the antigenic preparation of cv. UPSM-19. Since the indirect ELISA tests were made under the same condition and with atleast three repetitions of each combination it appears that these observed antigenic disparities as reflected in their OD. values developed as a result of antigen antibody reaction have some significance in the basic compatibility of host (Glycine max) and pathogen (F.graminearum) .

CRA was also detected in crude preparations and purified preparations from mycelia of Phytophthora infestans (races 4 and 1,2,3,4,7) with antisera of potato cvs. King Edward and Pentland Dell in concentrations lower than 50 µg protein/ml (Alba & DeVay, 1985) using indirect ELISA. Antiserum raised against Phytophthora fragariae detected homologous soluble antigen at protein concentrations as low as 2 µg/ml (Mohan, 1988). Indirect ELISA could also readily detect CRA in semipurified mycelial preparation of B.carbonum at concentrations ranging from 5-25 µg/ml with antiserum dilution 1:125. In cross reaction with antiserum of susceptible tea variety (TV-18) with antigenic preparation from B.carbonum (isolate BC-1) higher absorbance value was detected than the reaction with resistant variety (TV-26) of tea (Chakraborty & Saha, 1994). Based on these findings it can be assumed that indirect ELISA may serve as an important technique to detect cross-reactive antigens, to determine their properties and to investigate their properties and to investigate their possible role in host-parasite interactions, even in those interactions where conventional serological

techniques have failed to detect (Johnson, 1962 ; Carroll et.al., 1972).

The involvement of CRA in host-parasite compatibility has been discussed by several authors (DeVay et.al., 1967, DeVay and Adler, 1976 ; Chakraborty, 1988; Lyons and White, 1992) and is strongly supported by results of the present investigation. These results are also in-conformity with those of previous workers (Palmerly and Callow, 1978, Alba et.al., 1983; Alba and DeVay, 1985) who suggested that not all CRA contribute towards host-parasite compatibility but rather that only certain key CRA are important .

Changes in antigenic patterns were also detected in susceptible soybean cultivar (Soymax) after chemical induction of resistance. In this case, one common antigenic substance was missing from the uninoculated sodium selenite treated roots while two common antigenic substances were missing from the uninoculated sodium azide treated roots as evident in the immunoelectrophoretic tests. These change increased the antigenic disparity between treated roots and the parasite, and consequently the resistance of soybean plants(cv. Soymax) to F.graminearum increased to a considerable extent. In this situation sodium azide or sodium selenite appeared to act as a "Conditioner" of the plant cells which responded to infection by accumulating greater amount of phytoalexin (glyceollin).

An antigenic disparity in the susceptible soybean cultivar (Soymax) after induction of resistance by sodium azide treatment was also detected by Chakraborty & Purkayastha (1987), who discussed the changes in antigenic pattern and their involvement in induced resistance of soybean to charcoal rot disease caused by Macrophomina phaseolina. In another

immunoserological studies Ghosal and Purkayastha (1987) demonstrated the alteration in antigenic pattern in susceptible rice cultivar (Joya) after treatment with gibberellic acid which increased resistance to seed rot disease caused by Sarocladium oryzae. Similarly cloxacillin induced resistance of soybean against Colletotrichum dematium var. truncata and altered the antigenic pattern (Purkayastha and Banerjee, 1990). These findings suggests that resistance could be induced in susceptible plants by increasing antigenic disparity by suitable treatment.

In the present investigation using antibodies indirectly labelled with fluorescein isothiocyanate (FITC) the location of CRA in cross sections of soybean roots of resistant (UPSM-19) and susceptible (Soymax) cultivars and fungal cells (F.graminearum). Treatment of mycelia and conidia of F.graminearum with antiserum to roots of cv. Soymax and using indirect staining with FITC indicated that CRA was mainly present in young hyphal tips and in patch like areas on conidia. The results are also in conformity with the work of DeVay et.al. (1981a) involving treatment of conidia and mycelia of Fusarium oxysporum f.sp. vasinfectum with antisera to cotton.

Cross sections of soybean roots (cv.Soymax) treated with antisera of F.graminearum and then reacted with FITC conjugate developed bright fluorescence which was concentrated mainly around epidermal cells, the endodermis and xylem elements and was distributed throughout the cortical tissues; cell walls appeared to be the main cellular location of CRA. In roots of cv. UPSM-19 fluorescence was noticed only in the epidermal cells and cortex tissues.

The tissue and cellular location of major CRA shared by cotton and Fusarium oxysporum f.sp. vasinfectum was

determined by DeVay et.al. (1981a). Cross sections of young cotton roots with antiserum to F.oxysporum f.sp. vasinfectum and followed by an antirabbit globulin specific goat antiserum FITC conjugate exhibited strong fluorescence at the epidermis and xylem tissues indicating a general distribution of CRA determinants in roots. FITC labelled antibodies for races of P.infestans were also used to detect CRA in potato leaf sections (DeVay et.al., 1981b). In cross section of tea leaves (TV-18), cellular location of CRA shared by B.carbonum was evident mainly around epidermal cells (Chakraborty & Saha, 1994).

In the present host parasite system, the fungi F.graminearum infect and colonise the root tissues of both the resistant and susceptible cultivars but disease resistance of the host (Glycine max) is not expressed until the parasite invades the vascular tissues. Rather than search for a role for CRA in interactions of host and parasite within the realm of gene-for-gene relationships, several studies have provided evidence that the time of CRA involvement in basic compatibility phenomena is probably during the early cellular interactions of host and parasite when an exchange of metabolites may occur (Andrews, 1975) and induce a compatible or an incompatible interaction. A dynamic role is visualised for CRA after passive recognition events have occurred, which also may involve CRA and a host lectin (Dazzo and Brill, 1977), but prior to specific gene effects. Subsequent studies of Dazzo and Brill (1979) confirmed by Bhagwat and Thomas (1980), described a recognition phenomenon dependent primarily on exopolysaccharide of Rhizobium trifoli and a polysaccharide on the surface of root hairs of Trifolium repens having similar cross-reactive antigenic determinants and reactivity with trifoliin, a lectin produced by the clover roots. However, following recognition, intracellular compatibility of nodulating Rhizobium species with host roots may also involve

CRA common to legume hosts and the bacteria. In a comparison of 8 legumes and 8 non leguminous plant species, Charudattan and Hubbell (1973) found that all 3 species of Rhizobium tested shared CRA with the legumes but not with the other plant species.

DeVay and Adler (1976) suggested that common antigens are constitutive components of the cells of both host and parasite. Selection of parasite by host or vice versa may be controlled to some degree by fortuitous homologies of their genomes. Where there exist similarities for synthesis of cortical cell component, a compatible relationship would result, where as lack of homology would either repress metabolic processes or trigger the formation of metabolites which are toxic to cells of both host and parasite. If common antigens or cross reactive antigens (CRA) have a functional role other than in recognition phenomena, it probably will be found in the infection process and be subject to the overriding effects of substances such as phytoalexins or other inhibitory substance already present in host tissues or induced by parasitic micro-organisms (DeVay et.al., 1981a). Physiological function for CRA in host-parasite interaction is not clear. However, it can be stated that CRA may form a continuum between cells of host and parasite that favours the progressive growth and establishment of the parasite.