General defense system in the plant kingdom III.

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Summary: Our observations regarding the symptoms not fitting into, significantly differing from the hypersensitive defense system, which we noticed during the judgment of several plant species, symptoms provoked on several million plants have constituted a unified entity. They have provided evidence for the existence of a different plant defense system. We called this so far unknown basic response of plants to biotic effects as general defense system. This system defends them from the attack of numerous microbe species in the environment.
The evolutionary intermediate phase between the general and the specific, the two defense systems is the susceptible host–pathogen relation. The vertical resistance system of plants escaping from the susceptible host–pathogen relation, based on specific hypersensitive reaction also suggested the existence of a more original, general defense system and the susceptible host–pathogen relation developed as a result of the collapse of that system.
The evolutionary relation of the two defense systems is proved by the only recessive inheritance of the older general defense system and in the majority of cases dominant hereditary course of the specific defense system. In our experiences, the modifying genes of the recessive general defense system, in most cases, are behind the specific defense systems, which are known to have monogenic dominant hereditary course and react with hypersensitive tissue destruction. This seemingly striking genetic fact is explained by the following: the general defense system less dependent on environmental effects regulates much faster pathophysiological reaction than the specific resistance genes strongly dependant on environmental effects coding dominant hypersensitive reaction.
The general and specific defense reactions, the processes excluding the microbes attacking plants with compacting of cell growth and tissue destruction, which mean two opposite strategies, building on and regulating each other constitute the entity of resistance to plant disease.

Key words: *Capsicum, Phaseolus, Lycopersicum, Xanthomonas, Pseudomonas, Tobacco mosaic virus, Tomato spotted wilt virus,* artificial infection, new resistance, general defense system (*gds* gene), hypersensitive reaction, evolution, sugar content

Introduction

The susceptible species produced in the improvement period, resulting in bigger, nicer, abundant crops and taking into account other consumption aspects, but ignoring the disease resistance of plants, caused very great epidemics. The way-out from this situation was provided by the discovery of the hypersensitive reaction ensuring the disease resistance of plants *(Stakman,* 1915). Since this discovery all experts working in this field in the world, just as us have been thinking only of susceptible and hypersensitive prognostic symptoms during our thirty-year resistance improvement work. Plants, during the hypersensitive reaction, can prevent the propagation of the pathogen only through great tissue losses. Judging several million hypersensitive prognostic symptoms made us to think that plants must have a different, so far unknown basic defense system, which defends them from the attack of numerous microbe species in the environment by a different strategy, tissue compacting with cell growth.

Observation

Genes (*Bs-1, Bs-2, Bs-3*) ensuring resistance against *Xanthomonas vesicatoria* bacterium was built into the pepper variety *Early California Wonder (ECW)*. These nearly isogene lines are designated as *ECW-10, ECW-20, and ECW-30*. The numbers express only the time sequence of the descriptions of genes, because the prognostic symptoms determined by the genes refer to entirely different pathophysiological processes.

Our examinations concluded that, compared to the originally susceptible ECW variety, the pathogen, *X. vesicatoria* bacterium, was less able to multiplicate in *ECW-10*. This can be explained by the effect of *BS-1* gene ensuring hypersensitive reaction. *Bs-3* gene incorporated into the *ECW-30* line further increased the speed of hypersensitive reaction. The *Bs-2* resistance gene of the *ECW-20* line originating from wild pepper *Capsicum chacoense* species, also codes hypersensitive reaction. The general defense reaction inherited from the wild species and operating in spite of improvement selecting for hypersensitive reaction, however, delays the fast destruction and drying of tissues.

The general defense reaction is present in several *Capsicum* species. Item PI 163 192 contains this defense reaction the most fully in C. *annuum* species, wherefrom the resistance gene *Bs-1* was also derived. During the breeding of *ECW-10* line containing *Bs-1* gene, belief in the exclusivity of hypersensitive reaction ensuring disease resistance might have led to the ignorance of the general defense reaction. It is, however, unprecedented that the general defense reaction ensures perfect defense against the specific pathogen of pepper, *Xanthomonas. vesicatoria* bacterium species even without special resistance genes (*Bs-1*, *Bs-2*, *Bs-3*). We called this system *general defense system* and its gene symbol is *gds*.

Based on our genetic test and experiences in pepper breeding, *gds* gene proved to have basically monogenic, recessive hereditary character *(Szarka-Csillléry,* 1995, 2001a, 2001b). Examining the F_1 generation in numerous combinations (i.e. genetic backgrounds), we have concluded that other recessive and dominant genes, which may come from susceptible parents, can also modify the effectiveness of the *gds* gene. As a result of inoculation with *Xanthomonas vesicatoria* bacterium, *gds* gene was manifested in the F_2 generation at frequency of 25 per cent. Judit Mitykó, MBK, Gödöllő produced doubled haploid (DH) pepper lines from anthers of F_1 plants. Homozygous lines raised from individual DH plants showed different levels of resistance, which means random segregation of *gds* and the other modifier genes accompanying *gds*.

An important characteristic of the *gds* gene is that it is less dependent on environmental effects and is effective in both incompatible and compatible plant–microbe relations. So far an analogous general defense system has been found in tobacco, cucumber, beans and tomato in addition to pepper. Based on all this, we declare that all plant species must have general defense reaction, which defends them from microbes in their environment.

Conclusion

If during evolution, plants defended the attack of every microbe, with fast tissue destruction based on hypersensitive reaction against the specialized microbes, their pathogens, they would quickly lose significant part of their tissues, which would lead to full destruction. To avoid this, the general defense reaction, as an old characteristic tries to prevent all microbe attacks with tissue compacting of cell growth *(Figure 1)*. The evolutionary older, general defense reaction, since it has recessive hereditary course, is effective only in homozygote state and is not effective in heterozygote state. Consequently one of the numerous microbe species getting into contact with the plant selected to be a pathogen propagates in the plant without resistance. As a result, susceptibility as a state does not mean a gene, the gene of susceptibility, but on the contrary, the lack of a gene, the lack of one or both of the *gds* allelic pair. The cause of the difference among the susceptibilities of individual plants is traced back to the partial or total lack of *gds* gene and genes modifying its effect.

During evolution the host plant could escape from this state with special defense reaction effective only against the given pathogen. This is nothing else but hypersensitive reaction concomitant with tissue destruction. If the plant is forced for such a great sacrifice, this defense must be effective in all cases, both in homo- and heterozygote states. It can only happen if this characteristic, compared to *gds* gene, is inherited dominantly.

Tissue thickening and slight chlorosis caused by the general defense reaction and fast tissue destruction developing as a result of specific defense reaction prove the active defense processes of plants. On the other hand, the prognostic symptom developing in case of susceptible host–pathogen relation indicates the lack of the defense system of the host plant, which means the superiority of the pathogen. Therefore regarding the balance of the host–pathogen relation, the general and specific defense reactions refer to the superiority of the host plant, while susceptibility to that of the pathogen. The general and specific defense reactions are the resistant response of the host plant, while the symptom developing in case of susceptibility proves the lack of the resistance of the host plant.

We have examined the joint effect of the general and specific defense systems with the help of inoculation with *Xanthomonas vesicatoria* compatible with the pepper line containing *Bs-2* specific resistance gene and with *Xanthomonas phaseoli, Pseudomonas phaseolicola and Pseudomonas fluorescens* bacterium incompatible with it *(Figure 2)*.

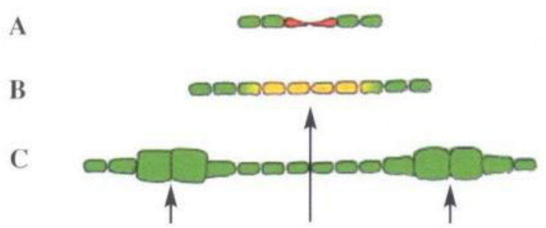

Figure 1 The strategy of plant cells excluding microbes, the old general defense reaction and in case of hypersensitive reaction effective against specific microbes, plant pathogens developed under constraint as a result of susceptible host–pathogen relation. **A** – specific defense reaction, **B** – susceptible reaction, **C** – general defense reaction

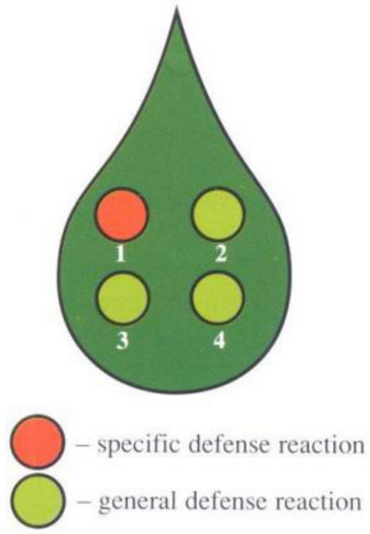

Figure 2 Symptoms developed on pepper leaf showing both general and specific defense reactions as a result of inoculation with *Xanthomonas vesicatoria* **(1)** compatible with pepper and *Xanthomonas phaseoli* **(2)**, *Pseudomonas phaseolicola* **(3)** and *Pseudomonas fluorescens* **(4)** bacterium incompatible with pepper.

The general defense system of the plant, with tissue thickening, excludes *Pseudomonas phaseolicola* producing exotoxin in course of pathogenesis and *Xanthomonas phaseoli* not producing exotoxin and also the saprophyte *Pseudomonas fluorescens* bacterium species and several microbes getting into contact with but not damaging pepper plants. This defense system ensures protection against the attacks of microbes in the environment, in the whole period of ontogenesis, in all phenological phases, on all plant parts from germination to destruction. These plant–microbe relations can be called incompatible relations because of the operation of the general defense system.

Pepper containing *Bs-2* gene had a specific hypersensitive reaction causing wine red discoloration to its pathogen, *Xanthomonas vesicatoria* bacterium.

Based on the examinations of pepper, we can conclude, the general defense system, in incompatible relations, while the specific defense system, in compatible relation constitute a unified entity of the disease resistance of plants. Examining the plant–microbe relation we can declare that incompatible relations regulated by the general defense system are more frequent than specific reactions based on hypersensitive responses.

Examining the whole defense systems of plants, the cell retaining reaction of the general defense system becomes understandable because if it responded to microbe attacks with tissue destruction, it would lose a significant part of its tissues. It uses hypersensitive reaction only as a last also resort against microbes specialized into pathogens. Consequently *plant reaction with cell compacting are quite frequent in nature, while reactions with cell destruction are quite seldom.* We must mention that the general defense system as an old characteristic can be restored by conscious improvement work in a way that it ensures protection also against microbes specialized for a given host plant, its pathogens.

The unity of the general and specific defense systems, constituting the whole defense system of the pepper can be traced well on pepper lines containing also *Bs-2* gene *(Figure 3)*. In addition to the cell retaining capacity determined by the system of *gds* gene and its modifying genes remaining intact, not destroyed during improvement, cell destruction caused by specific defense reaction is effective ònly to different extent. *The extent of the specific defense reaction appearing in hypersensitive tissue destruction is determined by the general defense level of the given pepper line.*

The inoculated tissues will thicken, as a result of the general defense reaction and only light wine-red discoloration refers to the presence of the specific defense system. Hypersensitive destruction of the inoculated tissues will take place only in cases, when the general defense reaction of the pepper line is on low level. Going from above down on the prognostic symptom series compiled to show the effect of the two defense systems compared to each other, tissue thickening based on cell compacting will decrease then disappear, simultaneously wine-red coloring and the extent of tissue destruction will strengthen.

The fact that the general and the specific defense systems are built on each other are proved by the appearance of L_1 specific resistance gene ensuring the *TMV* resistance of pepper in lines with different levels of the general defense reaction *(Figure 4)*. Two weeks after the inoculation, slight chlorosis develops on the cotyledons of the susceptible pepper lines (**A**) inoculated with *TMV* and mosaic patches referring to systematization of the virus on the foliage leaves backward in growth. On the cotyledons of the pepper line (**B**) with low level general defense system, which contain L_1 specific resistance gene, tissue destruction referring to hypersensitive reaction appeared on the fourth day following inoculation, which caused the destruction of the whole cotyledons, the fundament of the foliage leaf and finally of the whole plant. The same L_1 gene a few days later caused local lesion of definite edge on the cotyledons because the line (**C**) represented a high level general defense system. As a result of hypersensitive prognostic symptoms, cotyledons fell before the virus could have systematized. The healthy foliage leaves (**C**) significantly overgrew the susceptible infected control leaves (**A**).

The effect of the general and the specific defense systems regulating each other is proved by the fact that a specific resistance gene cannot develop local lesion without general defense system on adequate level. For lack of it, the whole plant is carried away by the infection. If the specific resistance gene is built into a plant with high level general defense system, local lesion will have definite edges. *The speed of lesion development, the diameter and character of the lesion are closely related to the level of the general defense system since hypersensitive tissue destruction is limited by tissue retaining capacity determined by the general defense system.*

Because of the narrow spectrum of the operation of the specific defense system based on hypersensitive reaction, the restoration improvement work, taking into account the existence of the *general defense system, opens up new prospects in resistance improvement. The general defense system by selection work can be raised to a level, which provides proper protection against specific pathogen species even in compatible relation without specific resistance genes.*

The general defense reaction of older recessive inheritance course based on cell compacting is effective in case of faster incompatible and compatible relations, too and is operative in the full temperature range necessary for the growth of the host plant. The evolutionarily younger specific defense system of dominant inheritance course based on hypersensitive cell destruction, works effectively only in compatible host-pathogen relation, in limited temperature range and in the background ensured by the general defense system.

The development of ring-like symptoms around the point of inocultation has been explained by extraordinary speed of the general defense system preceding specific hypersensitive reaction *(Figure 5)*. For example, in addition to the diverging feature of the prognostic symptoms of tomato lines susceptible to *Tomato spotted wilt virus (TSWV)* infection

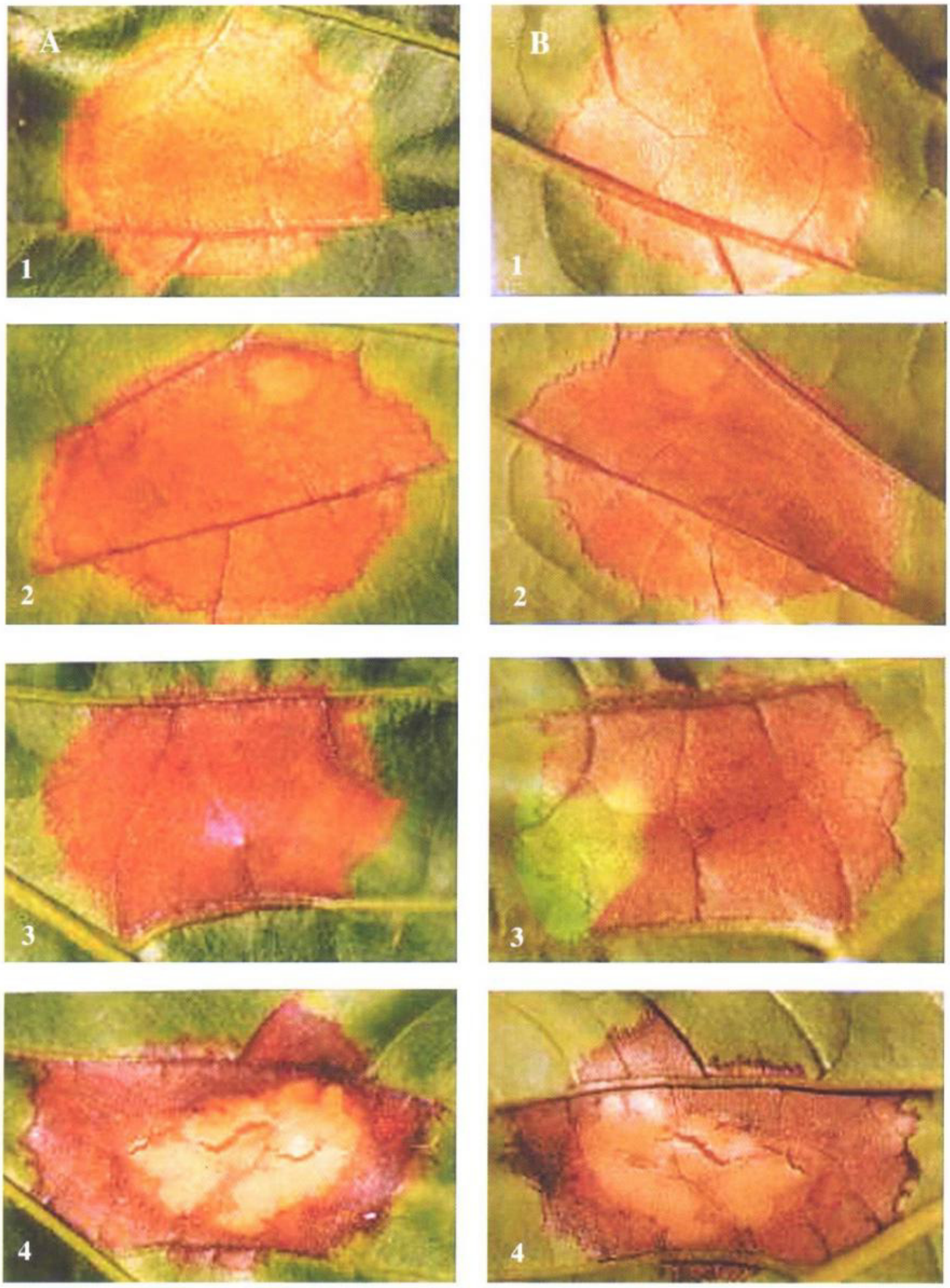

Figure 3 Symptoms on the adaxial (**A**) and abaxial (**B**) surfaces of the pepper leaves developing as the joint effect of the general and specific defense systems, the result of cell compacting and cell destruction. The effect of the general defense system decreases from above (**1-4**) downwards, while the effect of the specific defense system strengthens inversely proportionally.

and the ones responding with specific hypersensitive *(Sw-5 gene)* reaction, a common characteristic is the concentric, protruding spot of solid tissue around the infection point. These spots on the produce, independent of the ripening process, preserve the color of the tissues at the time of infection, which refer to the general defense system present also in tomato and the genetic background determined by its additional modifier genes. These kinds of changes aimed at the preservation of the infected tissues are clearly the characteristics of the general defense reaction. Although the

Figure 4 Reactions of pepper lines containing susceptible (**A**) and specific resistance gene (**L_1**) in a background provided by low (**B**) and high general defense systems (**C**) as a result of inoculation with *Tobacco mosaic virus (TMV)*.

general defense reaction notices infection, it is not able to block the specific pathogen and infection goes beyond the compacted tissue zone. In case of susceptible plant, although the compacted tissue will not die, the pathogen will overwhelm the plant. In accordance with their evolutionary role, the specific defense reaction of resistance plants will only start if the pathogen went beyond the compacted tissue zone, which means that the general defense reaction could not hinder the propagation of the pathogen. Thus ring-like symptoms are formed jointly by the general and specific defense reactions. The general defense reaction responds to all attacks against the plant immediately. Tissue compacting developing in this way either can or cannot hinder infection. If it cannot, specific defense reaction, beginning to work afterwards, has the task of protection. This is concomitant with hypersensitive tissue destruction. As a result, necrotic ring develops around the compacted tissue. In case of low level general defense system, because of specific defense reaction, necrotic spots deeply penetrating into the tissue will develop.

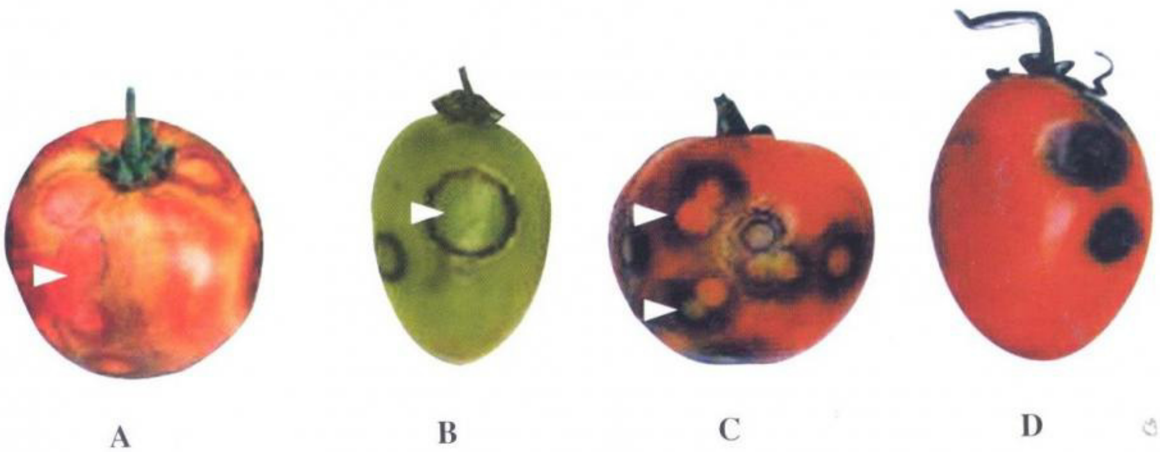

Figure 5 Symptoms of tomato lines (containing *Sw-5* gene) susceptible to *Tomato spotted wilt virus (TSWV)* infection and responding with specific hypersensitive reaction in the genetic background determined by the general defense system and its additional genes.
A – susceptible prognostic symptom, **B,C,D** – specific hypersensitive prognostic symptoms, – cell compacting referring to general defense reaction.

The relation of the general and specific defense systems is strongly influenced by temperature. The specific defense system based on hypersensitive tissue destruction provides defense only in the 15–30 °C range, while the general defense system works effectively also under extreme temperature conditions, outside the above range. The evolutionary process of building the general and specific defense systems on each other is clearly seen in host–pathogen relations examined in extreme temperature ranges *(Figure 6)*.

The bacterium develops water-soaking on species susceptible to *Pseudomonas phaseolicola* bacterium, which is surrounded by toxic halo-blight. The beans, resistant to the bacterium and containing specific resistance gene, respond with the development of purple-red lesion, which is hypersensitive tissue destruction referring to specific defense reaction in the 15–30 °C temperature range. The toxin of the pathogen causes hypersensitive tissue destruction and not toxic halo-blight around the watery spots on the beans leaves susceptible at very high, 45–50 °C temperature. At this high temperature, the specific defense reaction is hindered, but the general defense reaction sensitive to all biotic stresses responds immediately also in this temperature range, although the general defense system of the examined species is not able to block the propagation of the specific pathogen. In accordance with the evolutionary process, proving it also in this case, water-soaking referring to susceptibility developed in the infection point. The toxin produced by the propagating bacterium diffuse the surrounding tissue zone compacted with cell growth as a result of the general defense reaction. Beyond the compacted tissue zone, in the given temperature range the toxin of the bacterium causes hypersensitive tissue destruction in the plant containing specific resistance gene.

As a result of blocking the hypersensitive reaction regulated by the specific resistance gene with heat, the preserved evolutionary process has become visible. The microbe becoming pathogen and breaking through the general defense system develops susceptible host–pathogen relation with the given plant. The stress caused by the susceptible relation launches the hypersensitive reaction, but only if the plant has specific resistance gene. *The specific defense system will begin to operate only as a result of stress developing in case of biotic, susceptible host–pathogen relation exceeding the impact range of the general defense system. Consequently, the general defense system is not faster than the specific defense reaction but begins to operate earlier because of its lower stimulus threshold. Thus the specific defense reaction is not slower, but in accordance with its evolutionary task, high stress developing in case of susceptible host–pathogen relation is necessary to launch the process.*

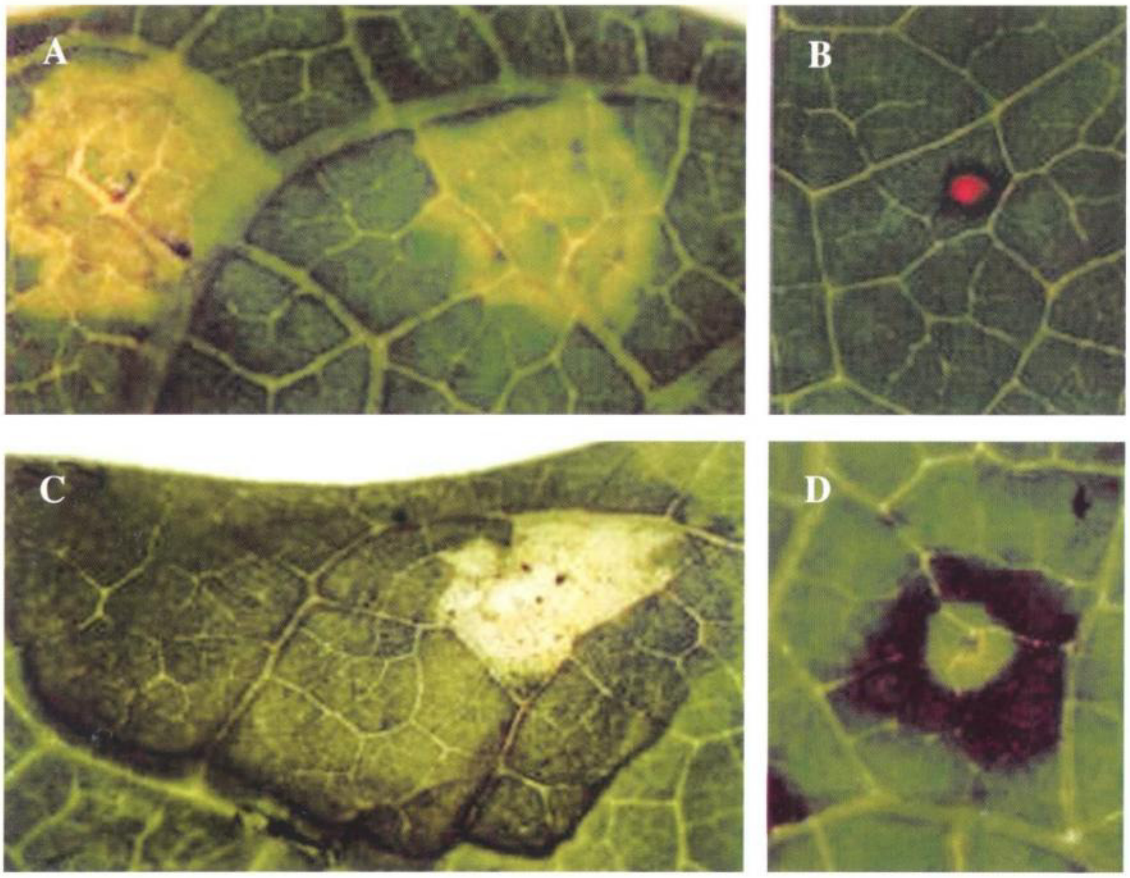

Figure 6 Specific defense reaction of susceptible (**A**) and resistant (**B**) beans in 15–30 °C range, and tissue spot referring to the presence of general defense reaction becoming visible as a result of limited specific defense reaction of beans susceptible (**C**) and resistant (**D**) in 35–40 °C range. The spot is surrounded by hypersensitive tissue destruction caused by toxin produced by bacterium propagating in the infection point.

Susceptible plants having general defense reaction and the ones giving special defense reaction respond to the toxins of the pathogens differently *(Figure 7)*.

The cotyledonary leaves of the bean, *Phaseolus vulgaris*, resulting from their physiological role, are not able to defend against microbes. To avoid the damage of microbes living in the soil, the hypocotyl, leaving the protecting seed coat in the soil, quickly lifts the cotyledons from the soil (7/1), in this way it protects the parts unable for defense reaction against the pathogens. This phenomenon also proves that within the general defense system, plants protect their different parts form the attacking microbes according to different strategies.

During germination, water-soaking (7/3) develops on the cotyledons of the bean seed (7/2) systematically infected with *Pseudomonas phaseolicola*. The toxin of the pathogen gets into the primordial leaves by translocation. The primordial leaves of the bean lines with high level general defense system, in spite of the toxin effect produced by the pathogen, preserve their dark green color, their tissue thicken and the leaves become deformed. Water-soaking caused by bacterium does not appear on it (7/4). The trifoliate leaves in underdeveloped form (7/5-6) become distorted to a great extent because of the systematizing toxin, their growth slows down, their color remains dark green, and water-soaking never develops on them. The foliage leaves slightly damaged by toxin (7/7) preserve their triple structure, do not become deformed or are deformed only slightly, their color is dark green; water-soaking does not develop on them. Plants, recovering from the impact of the pathogen, develop flowers and fruit (7/8) and ripe pathogen-free, viable seeds (7/9).

Seedlings (7/3) with water-soaking cotyledons sprout from the seeds infected with *Pseudomonas phaseolicola* bacterium of plants (7/2), having both susceptible and specific defense systems. Consequently toxic chlorosis and water-soaking referring to the presence pathogen develop on the primordial leaves (7/10). The shape of the primordial leaves is regular, but as a result of toxic effect increase and decrease of different extents are experienced. These severe prognostic symptoms are the consequences of the lower level general defense system.

The difference among the diseases of the trifoliate leaves of plants, which do not have susceptible, specific resistance gene, specific defense reaction, goes to the background ensured by the general defense system of different level. In case of the most severe damage, the foliage leaf fundaments will die because of toxin effect (7/11) or full toxic chlorosis and water-soaking (7/12) will develop on the trifoliate leaves backward in growth. The trifoliate leaves of beans plants with high level general defense system develop well and only partial toxic chlorosis and water-soaking develop on them (7/13). Water-soaking pod develops (7/14) on these plants and the pathogen is systematized into its seeds (7/15).

The first, second, probably the third foliage leaf fundament of the species with specific resistance gene die by hypersensitive reaction (7/16-18) as a result of toxin ascending from the infected cotyledons (7/3) and primordial leaf (7/10). This observation is the evidence that without the background provided by suitable general defense system, the specific defense reaction may be lethal. With suitable general defense reaction, the first trifoliate leaf rudiment do not die, do not show toxic chlorosis, are green, probably only the deformed shape indicates (7/19) the harmful effect of toxin. The bacterium is unable to systematize into these foliage leaves. These deformations are identical with the detail of Figures 7/5 and 7/6 showing the reaction of beans lines with high level general defense system. The foliage leaves of the plants recovering from the toxin effect (7/20) develop regularly and ripe bacterium-free pod (7/21) and seed (7/22).

Independent of the fact whether infection took place on the abaxial or adaxial side of the leaf, small crater like holes on the side of infection, and torosities referring to tissue compacting with cell growth develop on the foliage leaves of the beans lines with high level general defense system (7/7). Water-soaking, whose size is proportional to the level of susceptibility, develop on the beans plants not containing specific resistance gene (7/13). Only the trifoliate leaves of the plants carrying specific resistance gene are able to prevent the systematization of the pathogen with specific defense reaction (7/20). This reaction of the foliage leaves under natural conditions ensures adequate protection for the plants, although infecting their primordial leaves and pods artificially; water-soaking can be caused on them.

On this basis, we can conclude that the high level general defense system continuously provides protection against the pathogen, in every phase of the ontogenesis plant. Individuals without suitable general and specific defense systems are susceptible in every phenological phase. The specific defense reaction is operative only in the presence of adequate general defense system. If it is missing, which means the lack of general defense system counterbalancing hypersensitive tissue destruction with tissue compacting, the specific defense reaction becomes lethal.

The specific defense reaction can be launched only by the specific stress, which could not be inactivated by the general defense reaction. This specific stress is destroyed by the specific defense reaction with a one-off, big stress, hypersensitive tissue destruction. Tissue destruction happening in this way is a stress for the plant, which can be regulated by the general defense system all the time protecting and trying to preserve the tissue. Consequently the reaction causing hypersensitive tissue destruction does not become lethal and plays its role by making up for the deficiency of the general defense system.

Disease resistance of plants consists of the unity of the general and specific defense systems. Plants try to achieve disease-free state. The general defense system wants to prevent all biotic effects, and resulting from its operation we can speak about incompatible relation between the plant and the microbe. If the general defense system is broken through by some microbes, plants respond with susceptible reaction and compatible host-pathogen relation develops. The extent

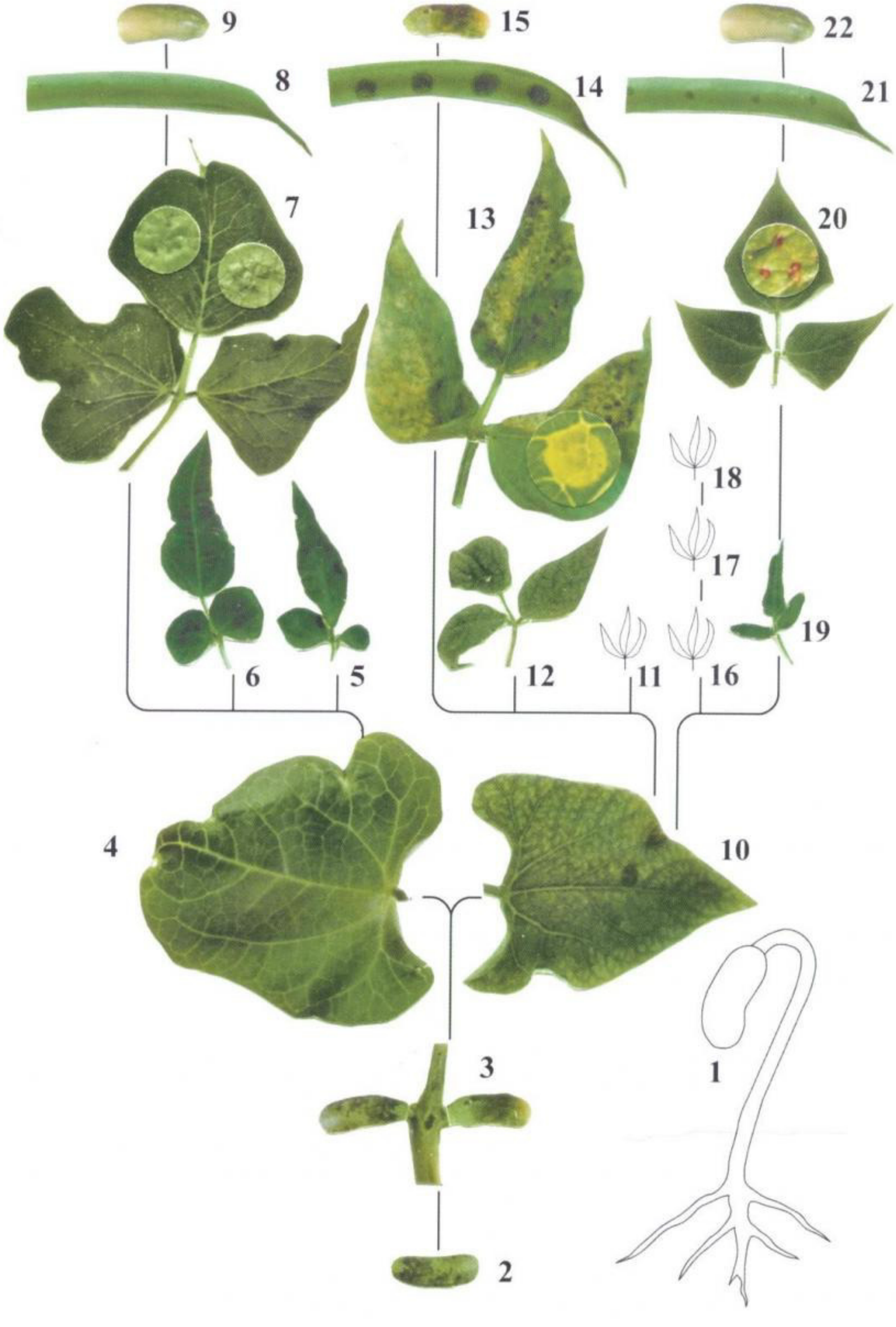

Figure 7 Symptoms caused, by *Pseudomonas phaseolicola*, on different parts of beans plants *(Phaseolus vulgaris)* having general defense reaction and giving susceptible and specific defense reaction

of susceptibility is dominantly determined by the level of the general defense system. The specific defense system can save plants from compatible pathogens. The specific defense system is only destined to correct the mistakes of the general defense system. The specific defense system is operative only building on the general defense system, without it, it is lethal. The specific defense system is made to operate by the stress caused by the compatible pathogen. If the general defense system is restored, the compatible host–pathogen relations will be again qualified as incompatible.

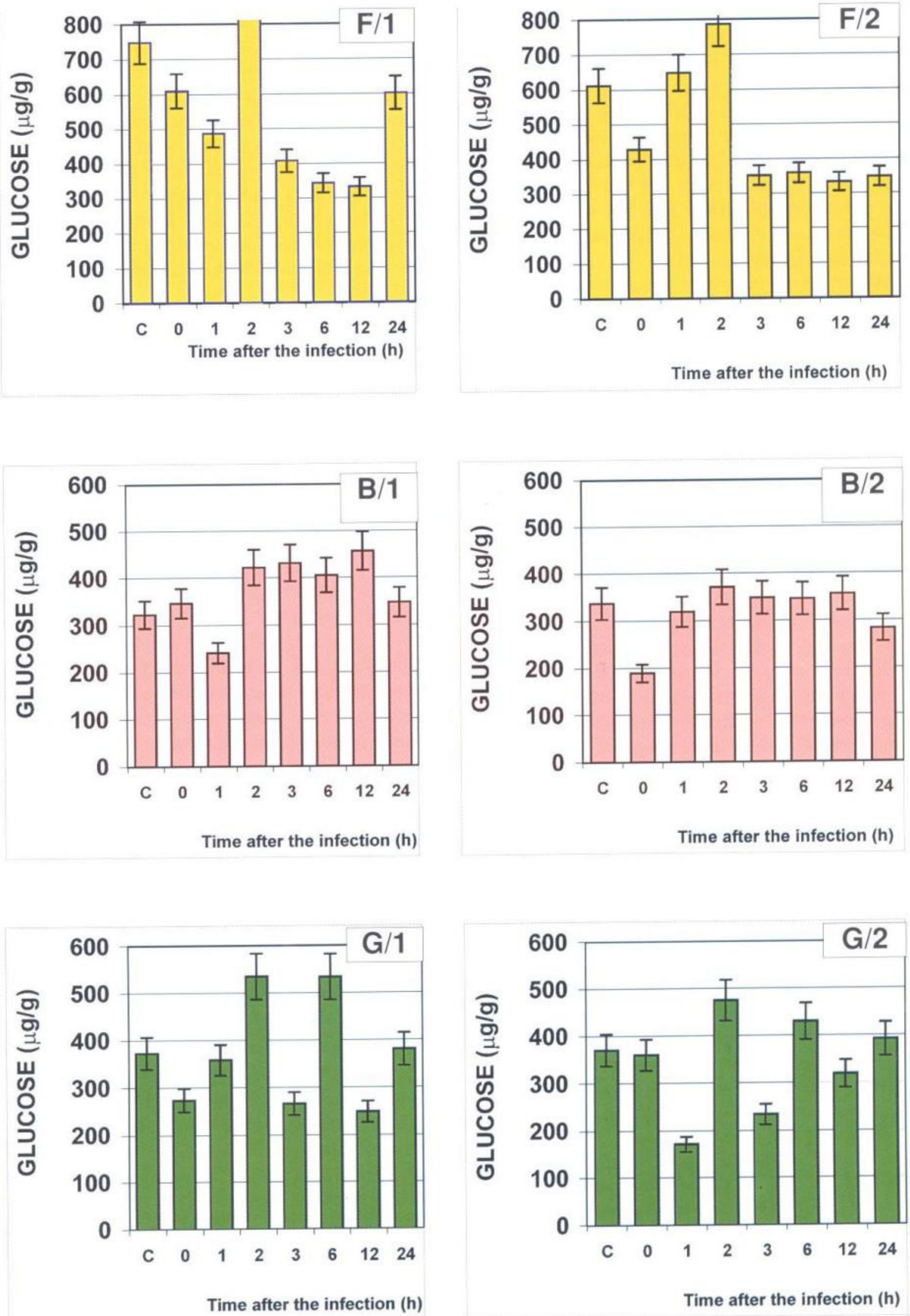

Figure 8 Changes in the glucose concentration of pepper lines which are of susceptible, specific resistance (*Bs-2*) and general defense system (*gds*), as a result of inoculation with *Xanthomonas vesicatoria* bacterium as a function of the period of time from infection in the inoculated and not inoculated tissues. C – control coming from not inoculated plants, **F** – susceptible plant, **B** – plant giving specific hypersensitive reaction, **G** – plant giving general defense reaction. **1** – not inoculated tissue, **2** – inoculated tissue.

In addition to histological changes in the prognostic symptoms, the examination of the plant physiological background provided further evidence to the different strategies of the two defense systems.

We have examined the glucose contents of pepper lines containing *Bs-2* gene coding susceptible (F), specific hypersensitive reaction (B) and *gds* gene regulating general defense reaction (G), leaf tissues (2) inoculated with *Xanthomonas vesicatoria* bacterium and leaf disc patterns taken from not inoculated (I), bacterium-free tissues beside the inoculated tissues *(Figure 8)*.

The separation of carbohydrate fractions with high-pressure liquid chromatograph (OPLC) has provided precise information on the quantitative and qualitative changes of glucose constituting the energetic basis of the plant *(Szarka E.* 2002).

In case of untreated control, the glucose level was the highest in the susceptible pepper line while it was the lowest in plants with special resistance gene *(Bs-2 gene)*, which gave hypersensitive reaction. The glucose content of the pepper line with general defense reaction (*gds* gene) was between the two.

The changes in the glucose content of the inoculated tissues of plants with susceptible, hypersensitive and general defense reactions were different both in time and quantity.

Examining the pathogenesis of *Xanthomonas vesicatoria* on susceptible plants, the well-known curve is obtained. The glucose content decreased in the inoculated tissues, and then increasing continuously, its quantity well exceeded that of the control. It went on until the glucose stock was exhausted. Then necrosis of the infected tissues took place. The change of the glucose content of the tissues around the inoculated tissues was characterized by similar curve but with phase delay because of the glucose transport.

The quantity of glucose in the inoculated tissues of the resistant pepper plants reacting with hypersensitive tissue destruction, following inoculation with *Xanthomonas vesicatoria* bacterium, has decreased significantly already in the few minutes between inoculation and first sampling, while the glucose content of the surrounding healthy tissues has not changed. After one hour, the glucose content was restored in the inoculated tissues, and then the effect of infection was not present during the 24 hours of the examination. The glucose content of the surrounding, healthy tissues showed similar changes with one-hour phase delay.

The glucose content of the inoculated tissues of plants with general defense system did not show any deviation from the control on the basis of the first sampling (0 h). The low glucose content of the samples taken from the surrounding, healthy tissues, however, makes us conclude that the infected leaf part is over a glucose minimum, since the glucose content of the neighboring, not inoculated leaf tissues could decrease only for its replacement. It is noteworthy that from the second hour of the pathological process, the glucose content of the inoculated and not inoculated tissues decreased and increased periodically but simultaneously until the end of the examination. This makes us draw the conclusion that glucose is used and replaced continuously.

The energy-saving glucose consumption of the specific hypersensitive reaction is one-off, and following quick tissue destruction, the process ends. The used sugar quantity probably burns until tissue destruction begins as a result of increased respiration. *The general defense reaction is faster than hypersensitive reaction, and contrary to specific defense reaction, operates continuously, therefore its glucose consumption differs both in quantity and in its course. The used greater quantity of glucose is utilized and built into the cells during the compacting, thickening of the inoculated tissues, which is growth with cell enlargement, with increased respiration.*

On the basis of plant reactions to biotic effects, we have concluded that the system of the disease resistance of plants comprises the unity of the general and specific defense reactions. The incompatible host–microbe relation is the result of the operation of the general defense reaction, while the specific defense reaction provides defense in the compatible host–pathogen relation. The susceptible host–pathogen relation indicates the lack of one or both of the defense reactions.

The general defense system reacts first to every stress and only if it is ineffective, the stress caused by the propagation of the microbe in the plant launches the operation of the specific defense system. Hypersensitive tissue destruction, as stress is regulated by the general defense system. The general and specific defense reactions, the processes excluding the microbes attacking plants with compacting of cell growth and tissue destruction, which mean two opposite strategies, building on and regulating each other constitute the entity of resistance to plant disease.

Since the cells of plants do not decay and do not renew during ontogenesis as it happens in the case of animals, the response with tissue compacting based on cell growth given to microbe attacks and other biotic stress remains a permanent memory around the infection point until the end of ontogenesis. The tissue zones defending these stress effects are immune to the new infections. In this way, the general defense system provides protection for plants not only in space but in time as well.

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