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Factors Influences Selection and Adaptation of Aphid to their Host Plant

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Abstract

Phytophagous insects are dependent on their host plants entirely or part of their life cycle. Host plant supplies food and shelter for their survival. Among the phytophagous insects, aphid is familiar as phloem feeders and act as a career of plant viruses to different agricultural crops. These cause huge economic losses every year in terms of both crop damage and their control measures. Instead of chemical control, it is better to inspect the relationship of aphid with their host plant like selection and adaptation pattern to develop an eco-friendly strategy to manage them. There are different factors of both host plant and aphid that determine the selection and adaptation of their host plant. Plant characteristics such as thickness of cuticle, presence or absence of waxy layer above the leaf surface, trichomes and nutritional status of plants greatly influence aphid species to select their suitable host plants. Moreover, insect factors like feeding behavior, ovipositional choice and their interaction with other biotas are important. However, the effect of global warming and environmental pollutions are most hot topic to analyze their impact on the aphid to select and adapt to their host plant. This review summarizes the main aspects of different factors that are regulating aphid's host plant selection and adaptation.

Keywords: Aphid; Abiotic and Biotic Factors; Host Plant; Selection; Adaptation

Introduction

Aphid is one of the important agricultural invertebrate pests in agricultural system having about 4500 species worldwide [1,2]. Although its life span is very short (around one month), higher reproduction rate enables them to continue their destructive effect to the crops through maintaining their population in the field. They not only damage crop through feeding on it but also contribute to introduce different viral diseases working as a vector [3,4]; therefore, it is becoming a major agricultural pest [5,6].

In modern agriculture, different insect management and control practices are existing. Such as, using pesticides it is possible to remove insect from agro-ecosystem within a short period. But insecticides have adverse effect in ecosystem services and functioning as well as human health [7,8]. Besides, continuous pesticides application develop resistance in insect body and minor insect converted into major one [9]. Environment friendly nonchemical control measure can serve the effective solution to reduce the incidence of aphid in the agricultural system. Manipulation of components of agroecosystems can be a good option to get rid from adverse effect of chemical control. Interaction of aphid with their host plant is a fundamental key to manipulate surrounding agroecosystem [10].

Host plants of an insect are those that supply food and shelter to an insect. As a phytophagous insect aphid dependent on their host plant to lead their life [11]. After selecting a plant, aphid have to adapt with it to get benefit from the host plant. Aphid ingests plant sap as their food from phloem part of the plant through slender piercing-sucking type mouthparts named stylets [12]. There are different factors such as climatic components, host plant characteristics and their defense mechanism, aphid itself characteristics like feeding habit, reproductive pattern, genetic factor both aphid and host plant may influence the host plant selection by aphid [13-17].

Plant morphological structures and chemical composition of plants are the first line of defense of plant against phytophagous insects [17]. Morphological features such as waxy layer above the plant surface, thickness of cuticle, presence of spines and trichomes influence aphid to select their host plant [17]. Besides, plant secondary metabolites, nutritional status of cell sap, water content of the plant cell interfere on selection of host plant by aphid [18]. Moreover, herbivore performance and quality of plants are affected with changing atmospheric components [19], that ultimately effects on their interactions. Elevated temperature and CO_2, moisture stress and environmental pollutants mostly SO_2, NO and NO_2 have a great impact on aphid population to choose their suitable host plant [20,21]. In addition, feeding and reproductive pattern of aphid and their interaction with other biota also determine the relationship between aphid and host plant [22,23].

This literature review was done to sort out the factors that stimulate phytophagous insect aphid to selection of host plant and realize the linkage among them. The summary from this review will be helpful to setup agrological environment in a farm to repel from aphid incidence.

Aphid Biology and Feeding Damage

Different species of aphid can be seen throughout the world, but variation of species is greater in temperate regions compare to tropical areas [24]. Aphid vary in their body length, body color and sometimes body features that depends on the nutrient obtain from the plant. Within animal kingdom aphid is the single organism that have capacity to produce carotenoid pigment that are usually found in plants [25]. Aphid species does not prefer all plant species as their host plant. In their host plant they feed on mostly all parts such as foliage, fruits, flower, and branches. They feed plant phloem cell sap through inserting their sucking type mouthparts (Figure 1). Mouth appendages of aphid are extended into a stylet bundle that cut the host plant tissue to touch the phloem site and at the same time stylet penetrate into the phloem. Aphid produces two distinct types of saliva. Proteinaceous and jellifying dense saliva around the stylet aids to create an intercellular route to the phloem for the penetrating stylets [26]. Another types of saliva secretion occur after penetrating stylet into the vascular system of the host plant [27].They excrete sugar rich substances familiar as honeydew that enhance the development of sooty mould in the economic part of plants and reduces the quality of product [28]. But honeydew attracts ants that save them from natural enemies of aphid. The life cycle of aphid is about 20-40 days. Their higher multiplication rate minimizes the duration of life span and retains their population in the ecosystem. Aphid possess sexual and asexual form of reproduction [29]. The female aphid lay eggs on young leaves and shoot and pass through a series of moulting to become adult. These mature aphid without any fertilization produce their daughter aphid. This form reproduction is known as parthenogenesis [30]. Although, the daughter aphids are not produced from the eggs they survive because they are surrounded by a transplant egg membrane. The offspring grow quickly and produce their next generation following the same process.

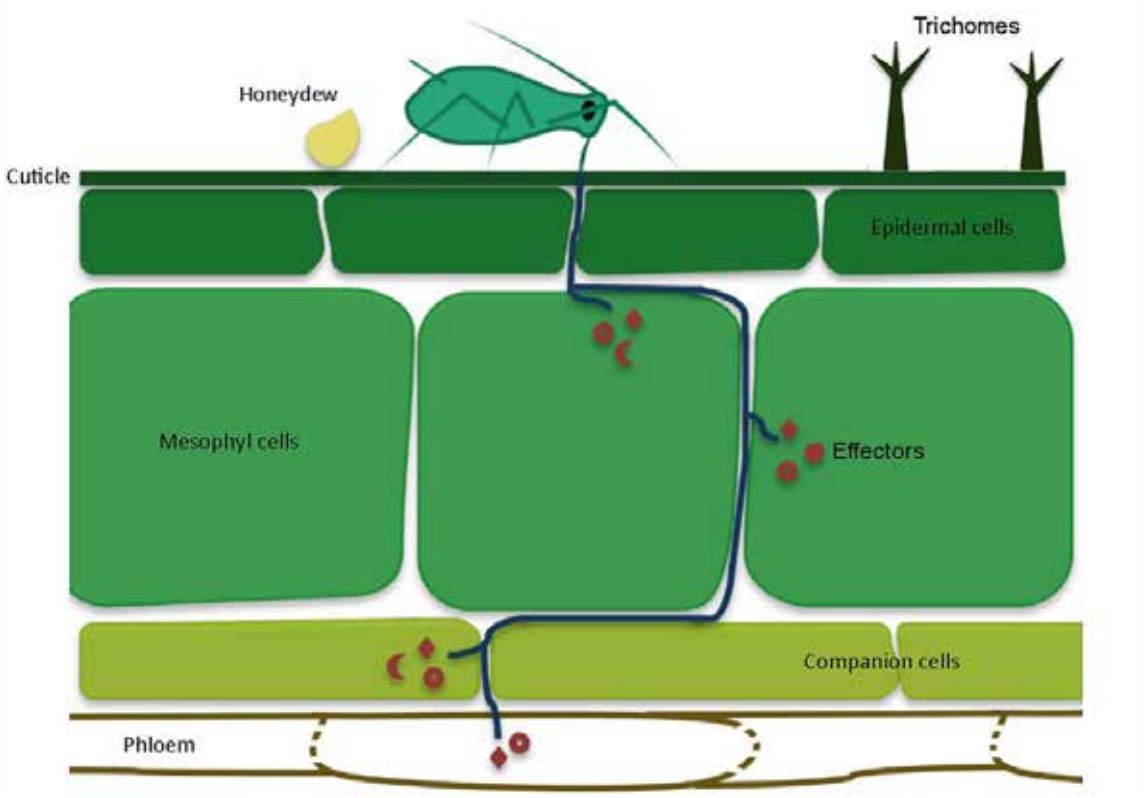

Figure 1: Cell sap sucking of aphid from the host plant [29]

Abiotic Factors

Climate change influence agricultural ecosystem including abundance and distribution of insects especially the periodic distribution of aphid is affected by climatic condition [31]. Most of the climatic components effect on the host plant selection and adaptation with their host plant.

Atmospheric CO_2 Concentration

Increased CO_2 concentration in the atmosphere individually can affects on crop physiology and plant herbivore interaction [32,33]. Crop damage by phloem sucking insect may increase with elevation of CO_2 [34]. The carbohydrate concentration of leaf increases and decrease

the nitrogen content and these changes reduces the nutritional quality of food [35]. As a result, aphid have to feed more to get same nutrition, that may influence them to change their host plant. Besides, elevated CO_2 can alter water content of foliage, leaf toughness, and concentrations of defensive chemical [36].

However, aphid may not be negatively affected by elevated CO_2 concentration compared to other insect groups such as chewers [37]. The possible reason for this difference is that aphids may be able to compensate for changes in host plant quality by altering feeding behavior or by synthesizing amino acids. O_3 concentration positively react with most of the phytophagous insect through reducing performance of natural enemies [38], ultimately increase herbivore distribution [39].

Temperature and Drought

Temperature is an important environmental component, that regulate spread, adaptation, growth and development of poikilothermic organisms [40]. There is a range of temperature where it can continue their growth and reproduction. The host selection process of aphid also influenced by changing temperature. Host plant changing aphid colonize in summer in herbaceous host plant but returning their woody host plant in autumn [41]. Because in summer season herbaceous plant provide more quality food compare to woody plant. Aphid can overcome the constraints imposed by higher temperature from migrating themselves from that area's host plant to other [42]. The density of aphid in an agroecosystem depends on the prevailing temperature of that area. In one study, it was observed that aphid presence and population build up regulated by temperature and reached in the peak in warm humid climate compare to cooler one on mustard (*Brassica juncea* L.) production [43].

There are some evidences that water stress promotes the incidence of some phytophagous insects [44]. There is a positive relationship between insect outbreaks and drought, nutrient-poor sites [45]. Besides, host plant temperature is also linked to the drought; it may enhance the growth and reproduction rate of insect. In drought stress host plants become yellowish and higher infrared reflectance that attract most phytophagous insect to the host plant [46]. However, growth and abundance of some sap sucking insect like aphid decline in drought stressed plant may be due to reducing turgor pressure of plant cells or prevalence of higher cell sap viscosity [47]. Aphid reply positively with intermediate water stressed plants [48]. As a result, aphid try to migrate from their previous colony to the suitable host plant where growth pattern of crop plant is good. In several studies, it was also recorded the effect of light on the adaptation of Aphid with host plant through manipulating microclimate as well as growth pattern of host plant [49].

Atmospheric Pollutants

Environmental components influence aphid to select their host plants [21]. Although, there are many researches already done using environmental components, but few studies were conducted to observe pollutants like SO_2 and NO_2 effect on aphid. SO_2 and NO_2increase the susceptibility of plant for herbivore and reduce the searching behavior of parasitoids. Atmospheric pollutants like SO_2, NO and NO_2 influence herbivore to choose their host plant through altering plant photochemistry [50]. Most studies show that insect herbivore rises in response to increase SO_2 and NO_2 [21]. Mechanism behind the susceptibility of host plant is the alternation of nitrogen metabolism. Also, $NO_2$and SO_2 can reduce the interest of natural enemies to control insects [51,52].

Host Plant Characteristics

Selection of host plant by insects is divided into steps 'host plant finding' and 'host plant acceptance'. After reaching to a plant site insect have to take decision that whatever accept or not. Different properties such as size, shape and color of plants interfere to select a host plant. Spread of insect towards the plant and adaptation also depends on host plant quality. The quality components of the host plant include levels of nitrogen, water content, defensive compounds, trace elements, carbon that positively or negatively effect on phytophagous insects.

Both external and internal plant characteristics have a great influence on aphid to select their host plant. Nitrogen and water content of leaves are two important considerable issues for an herbivorous insect. There are six times variations among the species considering young leaves damage despite of young leaves are higher herbivory than mature [53]. The rate of young leaf expansion linking to diet quality, including the cumulative effects of defenses and nutrition leading to the selection judgment of insect. Morphological features like waxy layer on the leaf, leaf thickness, the development of spines and trichomes provide defense services to plant from herbivore [54]. Internal factors such as nutritional status of plant cell, herbivore induced plant volatiles (HIPVs), secondary metabolites of plant affects on aphid to select as well as adapt to the host plant. There are some plant characteristics such as hair, thorns, trichomes and leaf thickness that provide direct defense against phytophagous insect or production of toxic chemicals like alkaloids, phenols, terpenoids, quinones, anthocyanins, that hamper in their development or kill them [17]. Sclerophylly means the hardened leaves that have direct role in plant defense against phytophagous insect including aphid through decreasing cell sap content and palatability [55]. In addition, granular trichomes discharge some secondary metabolites that act as poisonous or repellent to herbivore [56].

Both visual and chemical signals are used by phytophagous insect to detect host plant from a plant habitat [57]. There are many examples where indicate that volatile compounds from host plants helps phytophagous insect to recognize their appropriate host

plant [58,59]. For instance, in one study it was stated that, host plant odor carries a signal to invite herbivore from up to 100 meters distances [60]. But visual cues like leaf shape and color can be identified by phytophagous form 10 meters distance [61]. Within habitats, olfactory and visual plant cues continuously happen in combination and the relative significance of cue for herbivores during host location, which is sometimes difficult to assess [62]. Host plant detection and reception contact signal like non-volatile substances or mechanical incentives may be vital factors. For example, plant trichromes, leaf epicuticle waxes and non-volatile secondary compounds on the surface of the plant are known to trigger the rejection or acceptance of host plants for oviposition as well as for feeding [63].

In a habitat, the vegetational complexity is also determined by diversity of plant species of that area and it influences the phytophagous insect to select their host plant [64]. Diversity of plant species effect on volatile bouquet mixture in that habitat, as different plant secondary compounds are released from various plant species [65]. The presence of non-host plant in a habitat may indirectly affect phytophagous insect through natural enemies. Because, these natural enemies get alternative food, shelter from the non-host plant and ultimately leads to higher mortality of phytophagous insect [66]. Moreover, odors released from non-host plants might be more attractive compare to host species for natural enemies.

Characteristics of Aphid Itself

Aphid is one of the important phytophagous insects of majority of agricultural crops. Although there are many species of aphid present in respect to different crops such as pea aphid (*Acyrthosiphon pisum*), bean aphid (*Aphis fabae*), cotton aphid (*Aphis gossypii*); the damage strategy is more or less similar in majority of them. There are growing number of researches about the interaction between phytophagous insect including aphid and their host plants. As a sucking type insect aphid are dependent on their host plant, eventually they have to select and adapt host plant. Different factors like climatic factors, host plant characteristics, feeding habit of aphid, reproductive pattern, genetic factors and biotic interaction may influence aphid population to select their host plant.

Feeding Behavior

Aphid feed indirectly on plant vascular tissue by keeping high force in the sieve elements [26]. Feeding process of aphid consists of penetration of stylets into the leaf or stem and searching for vascular tissue [67]. Different physical and chemical attributes of host plant have a great influence in host plant choice by aphid considering their feeding behavior [18]. If the host plants are disallowed by aphid before feeding or entering stylet into plant cells, indicating plant toxicity. On the other hand, if aphid reject their host plants after penetrating their stylet or during feeding period, indicate nutritional quality or chemical compositional reason. Plant covered with a secondary metabolite known as indole glucosinolate (indol-3-ylmethylglucosinolate) into extra (4-methoxyindol-3-ylmethylglucosinolate) can provide a toxic defense to plant against insect feeding but it is local and non-systemic [68]. It is recorded that feeding choice of pea aphid (*Acyrthosiphon pisum*) is selected depending on host specific chemicals compare to escaping of deterrent [69]. Host acceptance of aphid based on their feeding behavior follow four sequential steps; prealighting performance, assessment of the plant surface and searching of sub-epidemic tissues, deep examining in the plant tissues and searching for the nutritional tissues, and assessment of the phloem sap of host plant as suitable for digestion [70]. The acceptance of host plant not only affected by phloem sap but also other tissue of host plant that creates obstacle to hunt for the phloem. In one study it was observed nitrogen status in host plant effect on host plant selection by aphid because it is an important factor for aphid growth [71]. Aphid try to avoid host plant with waxy leaf surface due to their inabilities to enter their stylet into the plant cell. Besides, host plant age also influence aphid to select their host plant as their feeding site. Previous infestation of host plant by another insect may have positive or negative effect on feeding choice of aphid. For example, susceptibility of peach (*Prunus persica*) plant to aphid (*Myzus persicae*) is increased when plants are settled by conspecific individuals and make suitable conditions for aphid feeding [72]. On the other hand, hetero-specific or previous conspecific feeding may have negative impact on aphid feeding in the same host plant.

Reproduction Pattern

Most of the aphid species are parthenogenetic and almost every aphid species able to lay fertilized eggs [30]. Aphid shows preference to select their host plant considering their ovipositional choice. The plant characteristics such as plant genotype, phenotype, physiology, architecture, distribution, density, chemical and physical cues are considered by phytophagous insect including aphid to select their ovipositional site [73]. In the summer period they choose woody hosts for secondary or herbaceous hosts, including vegetable crops of families Chenopodiaceae, Solanaceae, Cucurbitaceae, Cruciferae, and Compositae [74]. In the evergreen plant aphid generally lay eggs on the leaves [75]. But, in the deciduous host plant they lay their eggs on bud or young branches near to bud [76]. The physical and chemical properties of bud of host plant have a great influence on oviposition behavior of aphid [77]. But research in this site still in its infancy. Certain chemical signals may be involved in the antennae of aphid sensilla and reply to different volatile and non-volatile plant compounds [63,78]. For example, it is recorded after analyzing that about sixteen flavonoid aglycones present in birch buds. Female aphid looks for safety and mechanical support for their eggs and in this purpose, they select long bud mostly. The structural components of leaf like lipid and alleco-chemicals can also hamper or stimulate oviposition [79]. Plant volatiles also important in the sexual maturation and release of sex pheromones by the female aphid [80]. Besides, sometimes in searching purpose of male for female is also served by sex pheromone in addition with plant volatiles from the host plant [81]. In addition, natural enemies have direct influence on the ovipositional site selection of aphid.

Biotic Interaction

Aphid abundance and population growth are hampered by predators like ladybeetles and parasitoid wasps [82]. It not only reduces the aphid survival rate but also initiate escaping attitudes that decrease feeding and reproduction [83,84]. Sometimes parasitism alter aphid feeding choice. For instance, parasitism by wasp (*Aphidius ervi*) on pea aphid increase xylem consumption and reduce phloem sap feeding by that aphid [85]. The level of effect by natural enemies on aphid populations is greatly influenced by host plant of aphid. Secretion of plant volatile from host plant of aphid attracts predators and parasitoids of aphid, ultimately limits the aphid to choose host plant [86]. On the contrary certain aphid receives defensive substances from their host plant [23]. Host plant selection by aphid also influenced by antagonistic or mutualistic relationship with other insects [87]. Sugary excreta from aphid are consumed by ants and saves aphid from parasitoids and predators; provide a well-known example of mutualism. Aphid secretes honey dew that attracts ants in the host plant and saves them from natural enemies like predators and parasitoids. But there is a limitation that these ants can be act as predators if availability and quality of honey dew is not suitable for ants [88]. It seems as a debating topic since the presence of enough honey dew cannot confirm the existence of ant population in the host plant if quality of honey dew is not acceptable to those specific ants [88]. In addition, the abundance, distribution and activity of predators and parasitoids may also influence by changing environment that force on aphid population to change their colony from one plant to other [89]. The presence of non-host plant species in an agro-ecosystem also have to consider, as it supports natural enemies by proving food and shelter [66]. In most of the research it is not mentioned plant diversity surrounding the research field or plot. For example, a host plant may be suitable for aphid population, but the presence of non-host plant can support predators and parasitoids and ultimately deter on host plant selection.

With the increase of quality of host plant, the number of ants tending aphid may rise because the quality and quantity of honey dew may improve in a suitable host plant [90]. The honey dew chemical composition closely related to the phloem fluid of host plant and comprises with different organic acid, sugars, plant hormones, vitamins, alcohols, salt and amino acids [91]. There may also have negative or positive relationships with other phytophagous insects as well as other aphid species [92].However, interaction of aphid with other phytophagous insects are indirect and can be mediated by host plant quality [93]. The suitability of host plant is influenced by feeding guilds of other herbivore insects. As for example, aphid population can be reduced in tomato plant in the presence of caterpillar *Helicoverpa zea*. It may be due to induction of jasmonate-associating plant defense mechanism by the caterpillar, that hinders aphid survival and reproduction [94]. Nematode infested host plant also interferes in aphid population development through increasing parasitoids population. In addition, aphid species are very familiar for transmitting phytopathogenic viruses [95]. Aphid-vectored viruses can impose a selection pressure influencing host plant responses to these insects. Potato plant infected by potato leaf roll virus (PLRV) can generate changing behavior in aphid vector (*Myzus persicae*) to select their host plant [96]. However, may viruses increase host plant suitability and attractiveness for aphid species.

Genetic Factors

Host plant selection of different phytophagous insect is normally assumed to have a genetic basis [97]. The consequence of genetic connections on phenotypic progress are almost double. The genetic covariance can affect on reply of selection. In case of herbivorous insect, the genetic correlation on various host plants have a great effect on direction and rate of evolution of host plant characters [98]. Insects easily consider a plant as a host if the genetic correlation result is positive and high with respective host plant. It is recorded that, insect speciation driven by shifting and adjusting with new host plants. Moreover, feeding choice to host plant and host specific mating have a great role in starting the opportunity of speciation in the aspect of gene flow. Recent research observed in detail that, the mode and extent to which adaptation to various host plants may decrease gene flow between phytophagous insect populations [99]. It is proven that, loci linked to the performance of two plant species collocate on the genome in pea aphid (*Apis pisum*), indicating negative pleiotropy or genetic linkage [100]. In the nonappearance of genetic trade-off, the specialization can be changed, such as if the rank sequence of genotypes, fitness varies in the host plant. Divergent selection employed using ecological traits may affect in adaptive population distinction and generative isolation and affect differentially the level of genetic divergence beside the genome [101]. The genome of pea aphid (*Acyrthosiphon pisum*) has provided some understanding about candidate genes which allows aphis adaptation to their host plant [102]. Dissimilarities between races were observed in olfactory receptor genes and of them salivary proteins encoding by three genes [101], while it is unknown at which point in speciation these three gene variations happened.

Quantitative trait loci (QTL) is a widely accepted method of identifying resistant mechanism of host plant against aphid [103]. The QTLs have to analyze considering plant biochemical and physical traits that is resemble to distinct mechanisms, like pubescence and enzymatic movement of toxic compounds [104]. Different studies already done in mapping QTLs for resistance to aphid and majority of them are in annual crops [105]. In another studies, the connection between aphid resistance and some plant growth traits in apple was measured [106]. In addition of plant chemistry, the shoot growth features may also affect plant susceptibility to insects. It was found that significant resistant QTLs trait that is resistant to three aphid species and also found no similarity between the two kinds of traits QTLs [106]. Besides, it was identified that many QTLs that is resistant to aphid (*Myzus persicae*) and also for feeding and probing performance in wild peach [103]. Genetic properties of both insect and host plant also determine insect plant interaction. As different species of aphid choose separate type of host. While some crop specific genetic analysis already done through QTLs identification but there is a scope for further research on some important crops to analyze their genetic sequences [107].

Although a lot of research already have been done considering different component of plants and aphid behavior that influence host plant selection of aphid [108,109]. As aphid is phloem feeder and prefer young parts of plant, they would not able to stay in a plant throughout the life cycle. Future research can be done about up to which ages of a host plant is suitable for aphid so select and adapt.

Conclusion

Every season aphid causes a significant damage of different crops. Insecticides resistance is a most relevant issue to control aphid and people becoming more aware about bad impact of insecticides on the human health and the environment [110]. So, it is crucial to develop long lasting aphid management strategies. To overcome from this problem, it is necessary to achieve a clear concept about the factors that influences aphid population to select their host plant within an agro-ecosystem. In the schematic diagram (Figure 2) all possible factors responsible for the host plant selection and adaptation of aphid are presented. Further, researches are needed to disrupt their one or more favorable factors to control aphid infestation. Therefore, this review conveys a clear outline of plants, aphid and environmental stimulants to select host plants by aphid. Furthermore, this illustration will help to develop eco-friendly management strategies of aphid.

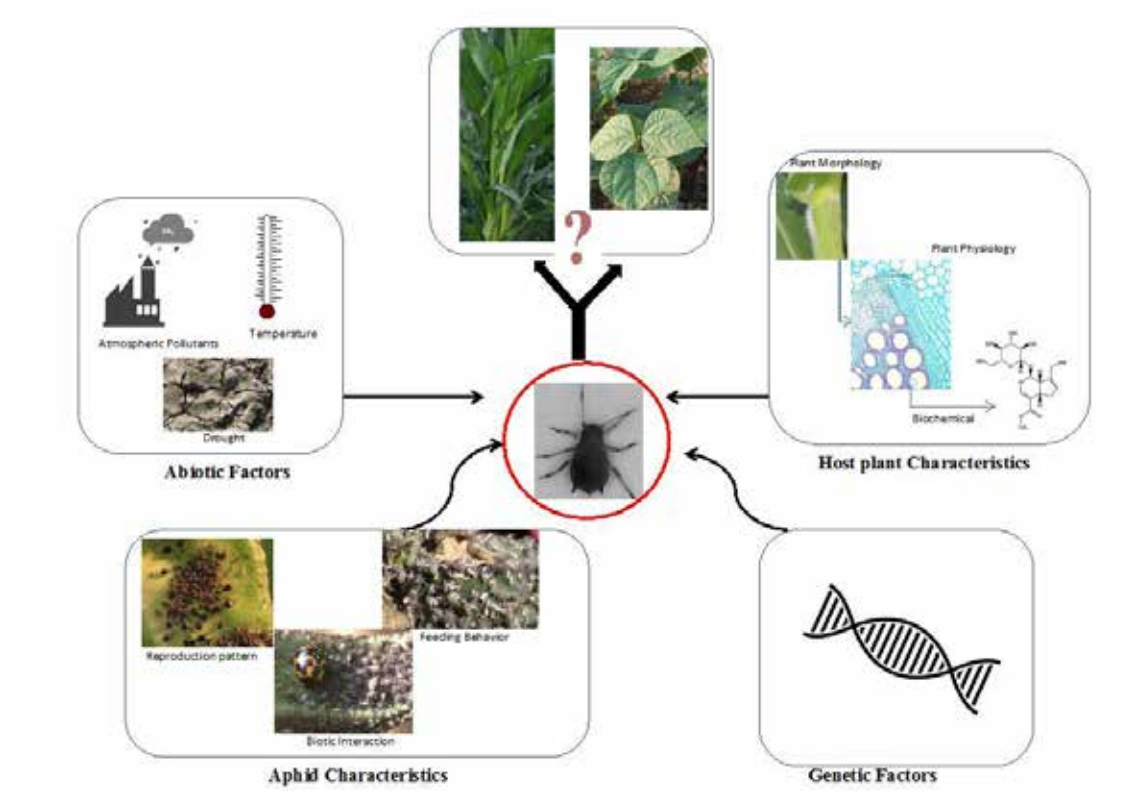

Figure 2: A schematic overview of the selection and adaptation factors of aphid to determine their host. Atmospheric pollutants, temperature and drought are the key elements of abiotic factors that force aphid whether or not to choose and stable in their host plants. Plants characters also contribute on aphid's host selection, mostly plant morpho-physiology and bio-chemicals. Apart from these factors plant and aphid genetics as well as aphid other characteristics take part in the decision-making process of aphid's host plant selection

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