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Review Article

Effects of crowding and stress on locusts, aphids, armyworms and specifically the hemipteran *Dysdercus fasciatus* Sign. (Hemiptera: Pyrrhocoridae)

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Abstract: Insect stress effects have been the subject of many reviews including heat, cold, and population stress. Production of winged aphids in unfavorable conditions or migrant phase of locust and armyworms, are reactions to crowding. Various crowding levels stress and treatment with low to high sub-lethal doses of insecticides at first had no effect but reduced *Dysdercus fasciatus* Sign. reproduction at higher levels. Stressors such as, crowding, toxins of sub-lethal doses of pesticides, host plant chemicals and environmental pollutants may produce comparable effects on insects. Stress may cause dispersion, migration, and insect pest outbreak. Locusts, aphids, armyworms and *D. fasciatus* react via plasticity to stressors including crowding stress by production of polymorphic phase. Neurohormones generally regulate the hormonal production of corpora alata, corpora cardiac and affect insect metabolism. This review relates the stress of crowding and insect phase to insect–plant relationships and the route to pest outbreak.

Keywords: Crowding, Stress, Locust, Aphid, Armyworm, *Dysdercus*

Introduction

Insects have to cope with insecticide toxins, natural enemies, different kinds of plant toxicants or any abnormal living conditions that may produce stress. Therefore stress is a reaction to various unfavorable conditions and can be density dependent. For example even microbial infections give stress signals to insects (Lanz-Mendoza, *et al*., 2002; Wu, *et al*., 2012), or rearing them in artificial laboratory conditions can increase their susceptibility to diseases (Sonleiter, 1964). Many insect species attain higher densities in simple environments with reduced biotic diversity (Price, 1997; Schoonhoven *et al*., 1998). Pest outbreaks are generally checked by natural enemies, insect disease epidemics or other unfavorable factors known as k-values (Varley *et al*., 1973). Insects destroy or damage all kinds of growing crops and other valuable plants. Everything about the life and behavior of insects is dependent upon chemical changes within their bodies. Neurohormones are the main factor responding to various stressors (Peric-Mataruga *et al*., 2006) and can reduce stress effects in insects.

Insect flight is regulated by metabolic pathways via neurohormones. Adipokinetic hormones (AKH) target the fat body for activating flight muscles in locust (Van Der Horst *et al.,* 1999). Crowding changes the physiology of locust by hormone secretion and can produce “phases” with different morphological and behavioral

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characters for solitary or gregarious populations (Uvarov, 1921; Ellis, 1963; Hodjat, 2006; Song, 2011). Only a few species of Acridoidea produce gregarious phases and in the gregarious forms they increase their dispersal activity after crowding. Field and laboratory experiments have shown that *Spodoptera littoralis* (Boisduval) are more destructive and march more when are reared in crowd (Brown and Swain, 1966; Hodjat, 1973). *Dysdercus fasciatus* and many other insects such as *Telenomus* spp, the egg parasitoid of *Eurygaster integriceps* Putton, 1881, are less active and do not fly when abundant food or their hosts are available near them in the laboratory (Hodjat, 1967). Experiments with a few cotton pests in Ahwaz, Iran showed that their outbreak was related to ecological environmental conditions. Germinating cotton seeds and young seedlings are frequently attacked by cutworms. Water stressed seedlings and hot dusty air increases the damage of mites (Hodjat, 1967). Insect damage to crops is considerably reduced in favorable weather conditions with high insect diversity (Samways, 2005). The coevolution and insect-plant-weed interaction in agro-ecosystem produces particular life cycles in response to local environmental conditions. Agricultural insect pest species generally have matched their life cycle to local crops and agricultural practice (Howard and Brlocher, 1998). In unfavorable conditions insect morphology and biometry changes and various forms appear in the field. Locust hoppers show marching behavior and reduce size or become darker by crowding (Ellis, 1963). Many other examples are given about insect morphological plasticity and production of various forms in reaction to stressors. (Hatfelder and Emlen, 2012; Ananthakrishnan and Whitman, 2005; Nylin and Gothard, 1998; Applebaum and Heifetz, 1999).

The aim of this review is to explain that ecological stress can cause pest outbreak (Barbosa and Schultz, 1967). Experiments with locust, aphids, armyworm and *Dysdercus* give some indication that their adult dispersion and migration is a response to stress of larval or nymphal crowding. Changing grasshoppers to locust is considered the first step of locust pest outbreak (Sword, 2003). Locust phase change is a result of population increase (Uvarov, 1921; Song, 2011; Hodjat, 2006). Phase is also suggested to occur in other insects such as armyworms (Brown and Swain, 1966) and *Dysdercus* (Hodjat, 1963).

The physiological changes of insect after crowding and under stress have comparable hormonal and metabolic pathways with other insects under stress (Showler, 2013). Resistance to toxins, toxicants and crowding or other stressors may have different physiological pathways in insects but ultimately they adapt or escape from stressful environment. Winged aphids are produced at high temperature, unsuitable host or crowding can be considered to be their reaction to ecological stressors. *Dysdercus, Spodoptera* and many other insect pests or parasites are not active flyers when reared in the laboratory with abundant food. Can food constraint or unsuitability be a factor for their dispersion and flight?

What is crowding stress?

Crowding is extra stimulation of increased number of the same species in limited area or cotainer of breeding vessles in the laboratory. Lack of sufficient room for free movement and continued contacts of individual insects may be stressful. Crowding affects various insect species differently. In most cases it increases the secretion of juvenile hormone (JH) and delay adult emergence. Table 1 show that the effect of crowding on various insects can be studied differently according to the purpose of research.

Crowding can change the insect physiology and stimulate some species to movement or alter their immunity to pathogens. Crowded insects are more susceptible to diseases. In mosquitoes, larval crowding reduces the ability of adults to transmit disease but in *Lymantria* crowding increases the resistance of larvae to nuclear polyhydrosis virus (NPV). The migratory locust is more resistant to *Metarhizium anisopliae* (Metschn.) biopesticide (Wang *et al.*, 2013). Cabbage looper, *Trichoplusia ni* (Hubner) activity, or its larvae to pupal transformation, is regulated by juvenile hormone (JH) (Jones and Hammock, 1983). *Tribolium freemani* Hinton reared in crowding conditions molts for more than six months (Hirashima *et al*., 1995). In *Tribolium castaneum* (Herbst) cannibalism was increased by crowding (Park, 1948). Crowding larvae of *Ephestia kuehniella* (Zeller, 1879) increased larval period but decreased emergence and survival rate (Bhavanam *et al*., 2012). In housefly, oxidative molecular damage and the rate of metabolism in relation to crowding and physical activity alter their size and life expectancy (Agarwal and Sohal, 1994).

Ecological stress effects on insect outbreak

Nutritional stress and crowding affect fitness component in insects. Environmental stressors and high level of crowding produce mortality on weaker individuals of insects. Survivors are naturally selected to tolerate the prevailing conditions (Kaliq *et al*., 2014; Ruuhola *et al.,* 2009).

Weather warming, reduction in rainfalls, dusty storms, reduction in diversity, inefficiency or lack of natural enemies are just a few reasons for pest outbreak. Insects enter diapauses or migrate to cope with some of the environmental stressors (Dean, 2013). In some cases, pupation, aestivation or migration is genetically programmed with no relation to stress (Price, 1997; Mattson and Haack, 1987).

Drought's physiological stress effects on crops have historically provoked outbreak of many agricultural pests (Mattson and Haack, 1987; Haack, 1987; Barbosa and Shultz, 1987). Many of fungal diseases such as root and stalk rots, stem cankers, and sometimes wilts and foliar diseases are much higher on water-stressed plants than on normal plants (Schoeneweiss, 1986). The evidence associating insects and drought is more circumstantial, consisting largely of observations that outbreaks around the world of such insects as bark beetles and leaf feeders are typically preceded by unusually warm, dry weather. There is also a consistent, positive correlation between insect outbreaks and nutrient-poor plants in dry conditions (Mattson and Haack, 1987).

Table 1 Some examples of crowding experiments extracted from various publications.

Insect species	Description of crowding effects	Reference
Tribolium (Tenebrionidae)	Virus diseases are activated in crowding. The physiology of crowded insect is altered. Transmission of disease at crowding conditions is increased.	Steinhouse (1958)
Chortoicetes terminifera (Walker, 1870) (Acrididae)	Phenotypic plasticity. Changing behavior from solitariness to gregarious phase. It also increases the expression of heat shock protein (hsp).	Chapuis *et al. (*2011)
Tribolium freemani Hinton	Increase the secretion of Juvenile Hormone Ester; JHE	Hirashima *et al.* (1994)
Subterranian termite	Group of less than 10 workers were insufficient for soldier differentiation. Soldiers were produced with groups of more than ten workers.	Mao and Henderson (2010)
Aedes aegypti (Linnaeus) (Culicidae)	Crowding larvae limit the infection by arbovirus better than uncrowded controls. Crowding stress caused an earlier emergence of adult mosquitoes.	Breaux (2014)
Acyrthosiphon pisum (Harris) (Aphidida)	Crowding increases the production in number of offspring. Phenotypic plasticity and polymorphic forms increased by crowding.	Weisser and Braendle (2000)
Lymantria dispar Linnaeus (Lymantriidae)	At higher densities they allocate more energy for disease resistance.	Reilly and Hajek (2008)
Propylea dissecta (Mulsant, 1850) (Coccinellidae)	When larvae reared at density of four per rearing vessel adults consumed more *Aphis craccivora* compared to other densities.	Pathak (2009)
Ceratitis capitata (Wiedemann) (Tephritidae)	Mortality increased by rearing larvae in crowd.	Carey *et al.* (1995)

High and low temperatures are threatening insects by the loss of water content from their body, therefore management of body water is a critical issue for insect survival (Delinger and Lee, 1998). The heat shock proteins (hsps) that are abundantly expressed in insects are important modulators of insect survival to heat. Biotic and environmental stressors induce the modulation of hormones to cope with unsuitable conditions (Zhao and Jones, 2012). In other words most heat shock proteins (hsps) function as molecular chaperones that help organisms to cope with stress. There is evidence that hsps and their encoding genes are involved in resistance to other ecologically relevant types of stressors such as those imposed by high population density (Chapuis, 2011). Environmental disturbance and drought also cause the outbreak of bark beetles (Rykiel *et al.*, 1988).

How insect physiology changes by stress?

All organisms including insects are exposed to stress (Wickens, 2001; Benoit, 2011; Bateson, 2012). Insects respond by respiration and metabolic changes to oxidative stress. Oxidative stress damage cells by lipid peroxidation and apoptosis. Free radical is toxic, and should be neutralized by antioxidants reactive oxygen species (ROS) in cells of insects, depending on their concentration, may act to remove parasites or toxins or create apoptosis (Vecera, 2011). ROS may also select population of *Acanthocelides obtectus* Say (Coleoptera: Chrysomelidae) for early or late reproduction types to adapt the population to different environments (Velki *et al.*, 2011; Lazarevic *et al.*, 2011).

Stress proteins or peptides change the hormonal pathways, and biochemistry of neurohormones. The central nervous system (CNS) needs oxygen to survive. Oxygen's role in insect metabolism is mysteriously very important in both prevention of organism from toxic materials and for fighting parasites. The end result of oxygen in oxidative stress is affecting insect size (Harrison *et al.*, 2010). Oxygen exchange in *Tenebrio molitor* L. at less than 21% affects the tracheal supply system (Loudon, 1989). Stress with anoxia condition causes cessation of nerve cells and insect is entering a "coma" as a result of spreading depression (SD). CNS coma in stressed insect can cause failure of body functions and surges of SD-like (K^+)o balance disruption (Rodgers *et al.,* 2010).

Schistocerca gregaria (Forskal) under low density is green and in cryptic form. At high densities they produce conspicuous yellow and black markings with morphological, physiological and behavioral changes (Wilson and Cotter, 2009; Harrison *et al.*, 2010; Showler, 2013; Cornell and Hawkins, 2003). Insect hormones are involved for activating anti-oxidative enzymes (Bendarova, 2013). Adipokinetic hormones (AKHs) regulate insect metabolism and provide flight energy in *Locusta migratoria* (L.). Three peptide structures: two octapeptides and one decapeptide are involved in onset of flight. They regulate flight energy by metabolic neurohormone that is released from corpora cardiacum (CC) (Van der Horst *et al.*, 1999; Bednarova, 2013; Peric-Mataruga, *et al.*, 2006).

Free radicals are quickly converted to water and oxygen to prevent damage to cells. They can have a beneficial effect in destroying damged cells or detoxifying poisons (Dean, 2013; Wu *et al.*, 2012; Lanz-Mendoza *et al.*, 2002; Komarov *et al.*, 2005; Even *et al.*, 2012; Peric-Mataruga, *et al.*, 2006; Zhao and Jones, 2012). For example free radicals are produced in *Anopheles albimana* Petrocchi for killing its parasite, Plasmodium (Lanz-Menoza *et al.*, 2002). In *Apis mellifera* L, stressors such as diseases, parasites, pesticides and poor nutrition are studied by many authors and reviewed by Even *et al.* (2012). They found that AKH or metabolic hormones are the main stress elements found in honey bee. The role in melanization of stressed insects is by production of phenol oxide (PO). It converts DOPA (3-(3,4-dihydroxyphenyl)-DL-alanine to quinones via their polymerization to melanins (Komarov *et al.*, 2005).

P450 enzymes are the first line of defense against xenobiotics in insects or their defense to plant allelochemicals and pesticides (Korsloot, *et al.,* 2004). The formal reaction of P450 is the insertion of one atom of oxygen into the substrate and the other atom being reduced to water. P450 reaction produces activated oxygen species such as superoxide, hydrogen peroxide, and water at the expense of NADPH (Nicitineamide Adenine Dinucleotide Phosphate) during catalysis as by-products (Feyereisen, 2005; Francis *et al.*, 2006). All activated forms of O_2 lead to deleterious reactions with DNA, RNA and proteins. However, the OH radical and O_2 are the two most reactive forms of activated O_2, and cause serious damage to cellular macromolecules including lipid peroxidation, protein oxidation, and DNA damage. These deleterious reactions are implicated in pathologies such as cancer, ageing, and cell death (Ahmad *et al.*, 1991; Felton and Summers, 1995; Yamamoto *et al.*, 2005). In relation to physical activity, housefly rate of metabolism alter their life expectancy (Agarwal and Sohal, 1994). Theory of ageing and free radical explain that metabolism in all living forms is achieved in cell mitochondria and breakdown of lipid by peroxidation. In other words the oxidized protein and free radical formation indicate ageing in organisms (Wickens, 2001; Agarwal and Sohal, 1994; Masoro and Austad, 2001)

What is oxidative stress and how it affects lipid storage in insects?

Superoxide dismutase (SOD), is a metalloenzyme that converts oxygen radicals to H_2O_2 in all aerobic organisms (Inze and Van Montagu, 2002). As organisms age the rate of radical conversions decreases and biological ageing is determined by the rate of cell apoptosis or necrosis (Masoro and Austad, 2001). Antioxidant enzymes such as SOD participate directly in dismutating the O_2^- radical, to the stable peroxide and oxygen (Ahmad *et al.*, 1991; Ivanovic and Jankovic-Hladni, 1991).

$2O_2^- + 2H^+ \longrightarrow H_2O_2 + O_2$

Catalase (CAT), on the other hand, targets the hydrogen peroxide and quickly converts it to water and oxygen:

$2H_2O_2 \longrightarrow 2H_2O + O_2$

Ascorbate peroxidase (APOX) which exists at low concentrations also scavenges hydrogen peroxide:

Ascorbic acid + $H_2O_2 \longrightarrow$ dehydroascorbic acid + $2H_2O$

As organisms age the rate of radical conversions decreases and biological ageing is determined by the rate of cell apoptosis or necrosis (Masoro and Austad, 2001). Lipids, including cholesterol are essential components of cell membranes and prevent insect from desiccation. Lipids also function as juvenile hormones and pheromones, and cholesterol is a precursor of ecdysteroid hormones. Lipid peroxidation is considered very injurious to cellular integrity and cause apoptosis (Bloomquist and Dillwith, 1985). Oxidative stress and antioxidants prevent apoptosis and regulate the physiology of gall insects to survive freeze and thaw winter periods. *Eurosta solidaginis* (Fitch) decreased oxidative stress enzyme activity while the larvae of *Epiblema scudderiana* (Clements) defend against ROS formation (Joanisse and Kenneth1996). Lindane is inducer of mixed function oxidase (MFO) and is essential in removing lipophilic xenobiotics from insect body (Rabideau, 2001). Xenobiotics similar to hormesis can reduce species populations and may change biodiversity.

Toxins and hormesis can cause stress and pest outbreak

Pesticides are applied at different doses to control insect pests. Doses that kill less than 50% of target pests are regarded to have sublethal effects on the survivors. Hormesis is the study of after effect of sublethal dose on pest survivors (Cutler, 2013). Pest outbreak after insecticide sprays as a result of eliminating natural enemies or insecticide drifts and studying insect physiology after recovering from sublethal doses are various kinds of hormesis studies (Cutler, 2013). General term "stress" is applicable for inhibition of Acetyle Cholin (ACh), neurosecretion of AKH or cytochrome oxidase (CO) histochemistry through mitochondria and oxidative stress (Sudhakaran *et al.*, 2014).

A full reduction of hydrogen peroxide to H_2O does not take place in stressful conditions and partial reduction of oxygen results in the formation of various forms of reactive oxygen species (ROS). Oxygen radicals may activate flight muscles and can result in leaving the stressful environment (Dean, 2013; Van der Horst *et al.*, 1999). The chill and high temperature injury effects in *L. migratoria* change the ATPase, SOD and catalyse (CAT) activity (Jing *et al.*, 2005). Crowding and sublethal dose effects of DDT and Dieldrin on *D. fasciatus* show that increasing the sublethal dose similar to increase of crowding decreased their reproduction but their wing fluttering was increased (Hodjat, 1963). Insecticidal toxins in plants and their effects as repellent and growth inhibitors on aphids can produce winged forms similar to crowding effects (Ibanez *et al.*, 2012).

The sublethal effects of insecticide spray on beneficial insects such as honey bee is also comparable to stress effects in other insects (Desneux *et al.,* 2007). In some cases low doses of pesticide have stimulatory effects on insects (Cutler, 2013). Habitat destruction and the stress of desert environment also reduce biodiversity (Foottit and Adler, 2009, Samways, 2005). Pollutants of all sorts, similar to sublethal effects of insecticides and toxins change insect physiology (Desneux *et al.*, 2007). Mimics of juvenile hormones can be used to control white flies. *Bemisia tabaci* (Gennadius) is resistant to conventional pesticides. They are treated by Pyriproxyfen which is known to be an analogue of juvenile hormone and is known to regulate the insect transition to various nymphal stages. White fly (Q biotype) may be controlled by spraying artificial JH. Toxic substances have morphogenic effects and can affect the expression of hundreds of genes. Sublethal concentration of the JHA may alter gene expression and the level of resistance genes (Ghanim and Kontsedalov, 2007).

Phase in locust and other insects and ecological stress

Phase polymorphism is density dependant (Song, 2011) and physical contacts or visual stimulation in *S. gregaria* produce marching movement in hoppers (Bazazi *et al.*, 2008; Rogers *et al.*, 2003). The transition between the two extreme phases is a multi stage molecular process (Applebaum and Heifetz, 1999) with changes in morphology and physiology that take several steps or even generations to complete (Hodjat, 2006). Only a few species of Acridoidea produce phase and in gregarious forms they increase their marching activity after crowding. Phase polymorphism and gregarious marching behavior with production of darker forms is common in many insects (Hatfelder and Emlen, 2012). Marching activity of larvae in *Spodoptera* species is comparable to gregarious phase of locust (Brown and Swain, 1966). *Schistocerca gregaria*, *Locusta migratoria migratorioides* Reiche and Fairmaire, and *Dociostaurus maroccanus* Thunberg; differ from common Acridudae (grasshoppers) because they produce gregarious phase. Phase polymorphism is accompanied by marching behavior (Ellis, 1963), color changing with more dark spots or bands on their body (Lecoq *et al.*, 2010; Hamouda *et al.*, 2011). Phase theory is a density – dependent phenomenon and in locusts it produces various morphs (Uvarov, 1921; Anstey *et al.*, 2009; Song, 2011; Lecoq, 2010). In second generation of rearing *L. migratoria* with more than 40 individuals per cage they produced gregarious phase characters. The symptom is at first by color and then morphological changes (Hamouda *et al.*, 2011).

Phase theory indicates that crowding and environmental conditions change the body performance of *S. gregaria, L. migratoria, D. maroccanus* and a few other grasshoppers. Variatin in color, morphology or activity of a few other insect species can also produce phase polymorphism (Anstey *et al.*, 2009; Song, 2011). These studies do not relate or measure the free radical to show stress effects on body functions (Hodjat, 1963, 1971; 2006; Lecoq, 2010). Phenotypic plasticity and phase is produced by crowding. Recent publications give some indication about phase in locust in relation to stress factor (Hodjat, 2006). Wu *et al.* (2012) relate the transition of locust phase to the effects of various metabolites. The lysophosphatidylcholines (LysoPcs) and free carnitine derivatives are the main chemicals responsible for phase polymorphism.

Crowding and repeated physical contact produced by either touching or jostling, elicits rapid and full behavioral gregarious phase in the absence of any other sensory stimuli in locust (Rogers *et al.*, 2003). Contact of hoppers in high population and neurosecretory hormones produce gregarization behavior in *S. gregaria* and increase the probability of cannibalism (Rogers *et al.*, 2003; Anstery *et al.*, 2009; Hodjat, 2006; Bazazi, 2008; Reynold *et al.,* 2011). The maternal effects and co-evolution interaction between insect and plants for seed beetles is reviewed (Fox, 1999; Mousseau and Dingle, 1991). Maternal effects from female crowding in *L. migratoria* changed their life history trait to gregarious phase. The females with a crowding history reproduced earlier and the offspring quality was increased (Chapuis *et al.*, 2010). *D. fasciatus* and many other insects such as *Telenomus*, the egg parasite of *E. integriceps,* are less active and do not fly when abundant food or their host is available near them in the laboratory (Hodjat, 1967).

Adaptive plasticity is a response to stress by physiological, morphological and behavioral traits. It is related to genetic and environmental effects (Nylin and Gotthard, 1998). Crowding stress might be the underlying molecular mechanism responsible for the appearance of alternative phase in locust. Free radicals are produced in haemolymph and the metabolic pathways of the solitarious phase differ from gregarious phase (Wu *et al.*, 2012). Crowded locust and production of gregarious phase might be similar to *Oncopeltus fasciatus* (Dallas) that migrate to follow its food plant, *Asclepias,* to escape from starvation stress. The natural distribution of *Oncopeltus* is from Canada to Argentina. Despite the presence of food plant, only short photoperiod of 8:16 (L: D) h at 25 °C produce diapauses in *Oncopeltus* (Dean, 2013; Mac Rae, 2010).

Prophylaxy and adaptive plasticity theories in relation to stress

Density dependent prophylaxis (DDP) has indicated that crowding, diseases, pollutants or toxins are stimulating the production of free radicals to prevent their delirious effects (Willson and Cotter, 2007; Mario *et al.*, 2009; Reynold, 2011). DDP is also believed to protect insect populations from the harmful environmental conditions (Wilson and Cotter, 2009; Reynolds *et al.*, 2011). Disease transmissions are positively density dependant. At high populations larvae of armyworms are more resistant to diseases (Reynold, 2011). DDP produced cannibalism or morphological plasticity in desert locust mainly through contacts by mechanoreception (Bazazi *et al.*, 2008; Rogers *et al.,* 2003; Dujardin *et al.*, 1999; Whitman and Agrawal, 2007).

DDP hypothesis explains that all living organisms seek biological or behavioral ways to escape distressful conditions (Wilson and Cotter, 2009). Disease causing agents, secondary metabolites or recovery from sublethal doses of insecticides can have similar effects and DDP may be a preventive measure (Wang *et al.*, 2013). Some insect species such as *Cimex lectularius* L. have obtained internal ability to survive and recover from strong environmental stress. They resist prolonged starvation and dehydration by increased temperature (Benoit, 2011). How did *Schistocerca americana* (Drury, 1770) which is a solitarious grasshopper change to *S. gregaria,* or desert locust that can produce gregarious phase? Developmental variation or “parental effects” might be one factor for separating the two species. Crowding in hoppers produces migratory adults. Evolution of differences in behavior of the two species might be due to selection of more parentally adapted populations (Sword, 2003). In other words escape from stress can cause genetic variation in populations for appearance of different traits (Howard and Berlocher, 1998).

Phase in *Dysdercus* and *Spodoptera* are also density dependant

Dysdercus species are active migrants and migrate in search for food within inter tropical convergence zones in Africa (Duviard, 1977). Reaction of *D. fasciatus* reared in crowd resembled those stressed by sublethal doses of insecticides or stressed by diet modification and starvation. *D. fasciatus* are reared on cotton seeds in the laboratory. They have highest fecundity and fertility when they feed on moist germinating seeds. Their reproduction and size was reduced after feeding on dried or boiled cotton seeds (Hodjat, 1972, 1963). The longevity, body size, egg diameter, and wing fluttering rate of *D. fasciatus* was measured in various experiments to compare laboratory effects of stress. They are active flyers in the field but they do not fly when reared in the laboratory. The results obtained by experiments with *D. fasciatus* are comparable to what is known about stress of crowding and phase in gregarious form of locust, *Spodoptera* or the cabbage looper (Hodjat, 1963; Henneberry and Kishoba, 1966).

Field and laboratory experiments have shown that *Spodoptera* species are more destructive and their larvae march together similar to locust hoppers in gregarious phase (Brown and Swain, 1966; Hodjat, 1973). Larvae *of S. littoralis* (Boisd.) that were reared at various densities were more active in crowded cages and darker in color. Larvae reared in isolation ~~they~~ were pale in color, very inactive, and hardly reacted to the presence of other larvae that touched them. Crowded larvae had reduced pupal weight, but their pupal period was increased and produced smaller adults (Hodjat, 1973). Damage of *S. littoralis* to cotton and various other host plants increased in dry but cooler autumn seasons in Ahwaz (Hodjat, 1967).

Crowding effects on aphids

Aphids (Homoptera: Aphidoidea) produce a number of different phenotypes in their life-cycle among which are winged (alate) and wingless (apterous) morphs (Vereschagina and Gandrabur, 2014). Aphids have two types of life cycles; A holocyclic or producing male and females and overwintering in egg form; An unholocyclic with parthenogenetic reproduction on herbaceous plants (Vereschagina and Gandrabur, 2014). Various factors are responsible to initiate the production of winged forms enabling aphids to escape from stress (Lukasik, *et al.,* 2012; Cornell, and Hawkins, 2003; Weisser and Braendle, 200; Khattab, 2007). The defense mechanism of cabbage plant to *Brevicoryne brassicae* (L.) is by accumulation and activation of stress enzymes (Khattab, 2007). Reproduction of parthenogenetic *Myzus persicae* (Sulzer) for phenotypes collected from various states in America produced different numbers of winged forms (Hodjat and Bishop, 1978).

The observed morphological plasticity in aphids is considered to be a response to escape from stress (Simpson *et al.*, 2011). Hormone pathways of many aphid species in response to plant secondary metabolites is considered to be the toxin effects (Giordanengo, 2010). Oxidative stress is studied through its physiological effects on body defense of stressed pea aphid (Lukasik, *et al.*, 2012). Experiments show that *A. pisum* on broad bean, which is not a preferred host, produce higher number of winged forms. They had increased oxygen radical in their tissues (Lukasik *et al.*, 2012). The production of winged aphids in colonies on citrus trees of north Iran increased when temperature and the clone population increased (Hodjat and Moradeshaghi, 1988; Hodjat, 1993). Water deficit makes it difficult for aphids to obtain nutrient by flowing through their proboscis. Prolonged water stress may alter host plant nutrients and affect the chemical combinations of amino acids and their volatile compounds. The water stressed plants can also affect the abundance of aphids on their host (Showler, 2013; Khattab, 2007). Proteome or protein involved in glycolysis is also involved in wing formation and host plant changes of *M. persicae* (Francis *et al*., 2006).

Insect and plant relationship

Continuous history exists between secondary metabolites production by plants to prevent insect attacks and production of new enzymes to detoxify the plant metabolites by insects. Plant and insect populations are in balance in natural habitats. Farming practices, use of pestisides or environmental changes such as weather warming, pollution or acid rains may change the balance and produc pest outbreaks. Plant oxidative stress also affects phytophagous insects and may cause pest outbreak (Inze and van Montagu, 2002; Ruuhola *et al*., 2009; Karban *et al*., 1989; Barbosa and Schults, 1987).

Variation in reproduction of insect pests might be due to the interaction of genetic and environmental effects (Eigenbrode, 1994). *Leptinotarsa decemlinea*ta Say prefers to lay eggs on hairy *Solanum sarrachoides* Sedt. rather than on potato (*Solanum tuberosum* L.), and eggs are less abundant on potato in the presence of *S. sarrachoides* (Caprinea, 2005). Terpenoids, flavonoids, alkaloids affect selection and change the suitability of the plant as food for insect. Lack of adequate nutrition in phloem and the inability to feed or the presence of tannins can be sufficient to prevent some insect from feeding (Capinera, 2005; Cornell and Hawkins, 2003).

Larger females usually produce more offspring in insects and stress reduces size and fecundity (Hodjat, 1968; Stillwell *et al*., 2009). Sexual size dimorphism (SSD) is common in insects and usually females are larger than males. The differences in size is selective and due to phenotypic plasticity (Stillwell *et al*., 2010). Aphids and some other Homopteran insects such as *Porphyrophora tritici* (Bod.) (Margarodidae) have two types of parthenogenetic or sexual reproduction depending on prevailing environmental conditions (Vahedi and Hodjat, 1995; Hodjat, 1993). Sexual differences and phenotypic plasticity also initiate production of dimorphic sexual populations with different traits and sibling species. Physiological variations in pest and plant populations, different injury potentials of insects and plant defense mechanisms, are only a few examples of insect plant relationships (Karban *et al*., 1989*)*.

Coevolutionary response to stress

Interaction between insects and plants started six million years ago when about 50% of insect species were feeding on plants. The relationship is beneficial for plant pollination and acquiring food for insects (Price, 1997; Mallet, 2007; Cornell and Hawkins, 2003). The response of insects to plant secondary metabolites, natural enemies or ecological conditions is by choosing various heritable traits among the population. Adaptation and selection of insects in response to diverse stressors is achieved by a set of physiological responses involving biogenic amines, neuropeptides, metabolic and CC or CA hormones (Even *et al.*, 2012). Symmetry is normally seen in most multicellular organism. Asymmetry is a trend in some population to diversify. Moller and Swaddle (1997) described variation and symmetry of development in animals and proposed that selectetive pressures of stress can initiate insect and plant to coevolutionary response.

Coevolution in agroecosystem is diversifying phytophagous insects for adapting their life cycles to various local cultivations. They may produce populations that by their refuge in weeds, other cultivated plants, or surroundings can pass the unsuitable conditions mostly in pupal or egg forms. Speciation is the result of long term genetic effect of environmental stress on various races or populations (Parsons, 1991; Roff, 2001). Plant phytochemicals are produced to prevent herbivores from feeding on them intensively. They appeared in an evolutionary time and resulted in escape and radiation in many plant and insect taxa (Cornell and Hawkins, 2003; Lee and Berenbaum, 1992).

The role of fumarocoumarin metabolite produced by plants is to prevent caterpillars from feeding intensively on them (Cornell1 and Hawkins, 2003). Therefore the response of *Papilio glaucus* L. or armyworms to furanocoumarin is their reaction to natural plant toxins. The promotion of the ion-to electron transformation of exogenous molecules in insect haemolymph and active metabolic pathways of furanocoumarin are similar to reaction to other plant allelochemicals (Mopper and Strauss, 1998). Resistance to toxins and toxicants is mediated by P450 gene family and effectively passed to their offspring by regulatory genes (Rewitz, *et al.,* 2007; Korsloot, *et al.,* 2004; Hodgson, 2004; Moriorty, 1999).

Evolutionary traits and reciprocal interaction of plant and insect is studied by many authors in detail. For example they changed the morphology of plants or mouth parts of pollinator insects (Pigliucci, 2005; Price, 1997). Sometimes mediators such as Arbuscular Mycorrhizal Fungi (AMF) may change crop resistance to pest attack or affect gene expression in insects (Vannette and Hunter, 2009).

Conclusion

Tables 2 and 3 are the author's deduction from the present results of research on the study of the stress effects on insects. In table 2 it is assumed that stress or autotoxication can cause phenotypic plasticity and result in diversity alteration. In order to measure and compare the reaction of insects after confronting toxic conditions more research is needed (Giordanengo *et al*., 2010; Showler, 2013; Simpson *et al.*, 2011). Table 3 also shows that more research efforts are needed to perceive and understand the differences between "normal" and stressful environments.

The following general conclusions may be deduced from this review:

1- The response of insects to intense crowding or harsh environmental conditions is comparable to their general reaction to cope or escape from stress.

2- Plasticity, dispersion and migration can be a reaction to crowding stress.

3- Pest outbreak and variation in population characters might also be insect reaction to stress.

4- Adaptation, selection and life cycle traits are evolutionary process reactions to stress.

Table 2 A list of further research efforts that are required on the subject of autotoxication, phenotypic plasticity and diversity to show how varius insects can cope with environmental stressors.

Autotoxication	Phenotypic plasticity	Diversity
Competition principles	Population characters	List of species in various localities
Insect-plant interactions	Asymmetry and stress	Districts list of species
Food chain and toxins	Morphometric ratios	Endangered or loss of species
Adaptation to host	Population genetics	Phase and bet-hedging
Resistance to pesticides	Speciation and host shifts	Stress effects on diversity
Ozone and climate change	Variation and forms	Population in agroecosystems
Monooxigenase detoxification	Cytochrome and gene expression	P450 genes and stress coping

Table 3 A general comparisons that can be perceived when organism is living under stress compared to normal developmental conditions.

Environmental stress	Normal conditions
Increase in variation	Homogenous populations
Movement and migration	Special population traits
Increased mortality	Adaptation of subpopulations
Genetic variation	Minimal allelic variation
Increased QTL differences	Minimal QTL differences
Local population extinction	Population stability
Dominant exchange of genes	Normal genotypic variation
Sexual dimorphism is common	Normal mixed breeding
Bet-hedging strategy is adapted	No need for bet-hedging strategy
Increased metabolic costs	Minimal metabolic costs
Character dissociation is common	Learning and population adaptation

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اثرات ازدیاد تراکم جمعیت و استرس بر ملخ، شته، کرم‌های برگ‌خوار و سن سرخ پنبه

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چکیده: اثرات استرس بر حشرات موضوع مروری مقالاتی از قبیل اثر استرس حرارت، سرما، و استرس تراکم جمعیت می‌باشد. تولید شته‌های بالدار در شرایط نامساعد، فاز مهاجر ملخ و رفتار حرکت گروهی در کرم‌های برگ‌خوار در واکنش به ازدحام جمعیت می باشد. سطوح مختلف ازدحام جمعیت و در معرض قرار گرفتن حشره در برابر سموم شیمیایی در ابتدا اثراتی روی سن سرخ پنبه *Dysdercus fasciatus* Sign. نداشت اما بعداً می‌تواند تولید مثل حشره را تحت تأثیر قرار دهد. در این مطالعه عوامل استرس‌زایی هم‌چون ازدحام جمعیت، مقادیر زیرکشنده آفت‌کش‌ها، ترکیبات ثانویه گیاه میزبان و آلودگی‌های محیطی که می‌توانند تأثیرهای قابل ملاحظه‌ای روی حشرات بگذارند مورد بررسی قرار می‌گیرند. استرس می‌تواند موجب پراکنش، مهاجرت، تغییرات شکلی یا طغیان آفات شود. انعطاف پذیری شکلی در ملخ، شته، کرم‌های برگ‌خوار و سن سرخ پنبه در واکنش به ازدحام جمعیت بروز می‌نماید. به‌طور کلی ترشح هورمون‌های عصبی، میزان هورمون‌های مترشحه از اجسام کاردیاکا و اجسام آلاتا و تغییر متابولیسم آن‌ها را موجب می‌شود. این مقاله مروری رابطه استرس تراکم جمعیت را از نظر تکاملی به رابطه حشرات با میزبان‌های گیاهی و طغیان آفات پیوند می‌دهد.

واژگان کلیدی: تراکم جمعیت ، استرس، ملخ، شته، کرم‌های برگ‌خوار، سن سرخ پنبه