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The Effect of Temperature and Nutrient on Developmental Biology and Physiology of Stored-Product Species of Coleoptera

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Review

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Abstract
Insect pests of stored crops damage agricultural products in the fields or warehouses and cause crop loss. For this reason, it is of great importance to protect the products in warehouses after harvest. Many chemical control methods are being researched to prevent the damage they cause to the stored product. As the negative effects of these chemicals used in recent years on the environment and living things have been understood, different methods have been started to be developed. Because insects adapt to the environment very quickly, they develop more resistance to the chemicals used over time. For this reason, the biology and physiology of insects should be well known in the fight against insects. The better the biology and physiology of an insect are known, the more new methods can be developed in the integrated control methods of this insect. Insects are poikilothermic organisms. In other words, since they are organisms dependent on changes in environmental temperatures, temperature is very important in their development. Another factor affecting the biology and physiology of insects is nutrient. Temperature and food together can limit insect developmental stages. While high temperatures prolong the developmental stages, it can have the opposite effect in the adult period. Or insects feeding on poor quality nutrient can affect egg and adult size or cuticle development, as seen in some beetles. In this review study, the effects of temperature and nutrient on the biology and physiology of storage product pest Coleopters were evaluated.

Keywords: Insects, carbohydrate, protein, lipid, food, storage pests, Coleoptera

Sıcaklık ve Besinin Coleoptera Takımına Bağlı Depolanmış Ürün Zararlısı Türlerin Gelişim Biyolojisi ve Fizyolojisine Etkisi

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Öz
Depolanmış ürün zararlısı böcekler, tarlalarda veya depolarda tarımsal ürünlere zarar vermekte ve ürün kaybına neden olmaktadır. Bu nedenle ürünlerin hasat edilmesinden sonra depolarda korunması büyük önem taşımaktadır. Depolanmış ürüne verdikleri zararı önlemek için bir çok kimyasal mücadele yöntemi araştırılmaktadır. Son yıllarda kullanılan bu kimyasalların çevreye ve canlılara olumsuz etkileri anlaşıldıkça farklı yöntemler geliştirilmeye başlanmıştır. Böcekler çevreye çok hızlı adapte olmaları nedeniyle kullanılan kimyasalara zamanla daha çok direnç geliştirmektedirler. Bu nedenle böcekler ile yapılacak mücadelede böceklerin biyolojisi ve fizyolojisi iyi bilinmelidir. Bir

böceğin biyolojisi ve fizyolojisi ne kadar iyi bilinirse bu böcekle yapılacak entegre mücadelede yeni yöntemler geliştirilebilir. Böcekler poikliotermik canlılardır. Yani çevre sıcaklıklarındaki değişikliklere bağımlı canlılar oldukları için sıcaklık, gelişimlerinde oldukça önemlidir. Böceklerin biyoloji ve fizyolojisini etkileyen diğer bir faktör ise besindir. Sıcaklık ve besin, birlikte böceğin gelişim aşamalarını sınırlayabilir. Yüksek sıcaklıklar gelişim aşamalarını uzatırken ergin dönemlerinde tam tersi etki yapabilir. Ya da kalitesiz besinlerle beslenen böcekler bazı kınkanatlılarda görüldüğü gibi yumurta ve ergin büyüklüğü veya kutikula gelişimini etkileyebilir. Bu derleme çalışmasında sıcaklığın ve besinin depo zararlısı kınkanatlıların biyolojisi ve fizyolojisi üzerindeki etkisi değerlendirilmiştir.

Anahtar Kelimeler: Böcekler, karbohidrat, protein, lipid, besin, depolanmış ürün zararlıları, Coleoptera

Introduction

Grains are the leading agricultural products that contribute economically all over the world. Agricultural products are stored in warehouses or silos before being delivered to the final consumer. The preservation of agricultural products in warehouses is an economically very important problem. During the storage period, the stored products may be unprotected against many pests such as insects, microorganisms, mites and fungi. Most of the crops are destroyed due to these pests. Among these pests, insects are the ones that cause the most product loss. The reason for this, they pass the developmental stages such as larva and pupa inside the seed [1]. Insects cause damage such as loss of product weight, loss of shape, decrease in nutrient amount, decrease in germination power and contamination of seeds in plant seeds [2]. In developed countries, 5-10%, and in developing countries, approximately 30% are damaged in this way [3]. 145 species of stored product pests belong to the order Coleoptera. This is followed by the order Lepidoptera, Psocoptera and Hymenoptera [4, 5]. In Table 1, some stored product pest insect species of Coleoptera seen in the world and in our country are given.

Insects are poicliothermic organisms. Therefore, temperature is one of the most important environmental factors affecting their metabolism and physiology. Stored product pests generally prefer at an ambient temperature of 27-33 °C and a humidity of 65-70% r.h. They cause very high losses under specified optimum conditions [1]. Generally, insects are not active at storage temperature below +10 °C and humidity below 10-12%. Their metabolism slows down when the temperature drops below 25°C, they cannot be fed below 17°C and they usually die below 10°C [1, 6, 7].

Temperature and nutrition are important factors affecting insect physiology. Recently, there are so many studies that food can alter temperature-related fitness in insects. For example, food quality can alter the physiological and biochemical reactions necessary for insect fitness [8]. Understanding these complex relationships between temperature and nutrient may be important to understanding the nature of individual and population-based responses of insects to changing environmental temperatures under different nutrient conditions [8]. Carbohydrates, proteins and lipids are vital for all living organisms. Insects either obtain these substances they need for growth and development from their environment or

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synthesize them through metabolic activities [9-11]. Insects can use these vital elements for growth, reproduction and development, as well as for pheromone synthesis etc. for communication purposes. Carbohydrates, one of these vital elements, serve as the primary energy source, while amino acids are found in the structure of enzymes that have a catalytic effect in cells. Lipids are a storage energy source. At the same time, they play a role in functions such as membrane permeability, egg production, pheromone synthesis [12-14].

Table 1. *Some stored product pests from Coleoptera [5].*

Species	Family: Order	Main Host
Sitophilus ganarius (Linnaeus, 1758)	Curculionidae: Coleoptera	Grain
Sitophilus oryzae (Linnaeus, 1763)	Curculionidae: Coleoptera	Grain
Sitophilus zeamais (Motschulsky, 1855)	Curculionidae: Coleoptera	Grain
Sitona crinitus (Herbst, 1795)	Curculionidae: Coleoptera	Grain
Tribolium confusum (Jacquelin du Val, 1863)	Tenebrionidae: Coleoptera	Grain
Tribolium castaneum (Herbst, 1797)	Tenebrionidae: Coleoptera	Grain
Tenebrio molitor (Linnaeus, 1758)	Tenebrionidae: Coleoptera	Grain
Latheticus oryzae (Waterhouse, 1880)	Tenebrionidae: Coleoptera	Grain
Tenebriodes mauritanicus (Linnaeus, 1758)	Ostomatidae: Coleoptera	Grain
Rhyzopertha dominica (Fabricius, 1792)	Bostrychidae: Coleoptera	Grain
Trogoderma granarium (Everts, 1898)	Dermestidae: Coleoptera	Grain
Oryzaephilus surinamensis (Linnaeus, 1758).	Silvanidae: Coleoptera	Grain, dry fruit
Cryptolestes ferrugineus (Stephens, 1831)	Cucujiidae: Coleoptera	Grain
Carpophilus hemipterus (Linnaeus, 1758)	Carpophilidae: Coleoptera	Dry fig
Lasioderma serricorne (Fabricius, 1792)	Anobiidae: Coleoptera	Tobacco
Acanthoscelides obtectus (Say, 1831)	Bruchidae: Coleoptera	Grain
Callosobruchus maculatus (Fabricius, 1775)	Bruchidae: Coleoptera	Grain

Chemical control is the most common method used to control stored product pests. But, in recent years, researchers have been trying to find environmentally friendly alternative methods due to the damage caused by chemicals to the environment and human/mammal health, as well as the resistance of insects to these chemicals. However, it is necessary to know the ecology, biology and physiology of the pests very well in order to find alternative methods and to protect the products. In this review study, the effects of temperature and food on the biology and physiology of storage pests from Coleoptera were evaluated. Understanding the effect of temperature and nutrient on the physiology of insects and evaluating their responses to changing environmental temperatures can enlighten on our strategies to fighting these insects.

The Effect of Temperature and Nutrients on Developmental Biology and Physiology of Insects Belonging to the Order Coleoptera in Stored Products

″Three temperature zones are defined for living organisms″.″The first is the Optimum Zone, where the development and reproduction takes place at the maximum level, and the second is the Suboptimum Zone, which is below or above the optimum zone where the living organism can complete its life cycle but its biological activities are lower [15]″.″The third is the Letal Zone, which causes the death of the living organism and is above or below the temperature values in the suboptimum zone [15].″

Temperature, humidity and nutrients are effective factors in the development and growth of insects. Generally, low temperatures and humidity prolong the development period in insects. High temperatures can have the opposite effect, while reducing growth rate and fecundity and increasing adult size [16, 17]. Temperature and nutrient are linked through the metabolism and energy requirements of insects [8]. Qualitatively and quantitatively insufficient nutrients prolong the development period, decrease the growth rate, adult size, fecundity, and cause some anatomical disorders in adults [9, 18, 19]. All ectotherms can change their nutrient preferences depending on the changing ambient temperature. This may be related to their physiological conditions, developmental stages or phylogeny [8]. Rho and Lee [8] determined the nutrient preferences of *Tenebrio molitor* Linnaeus 1758 (Coleoptera: Tenebrionidae) at different temperatures, stated that insects chose protein and carbohydrate equally at 25 and 30 °C, but only carbohydrates at 35 °C. Hashem et al. [20] conducted a study with *Oryzaephilus surinamensis* Linnaeus 1758 (Coleoptera: Sivanidae) at different temperatures (20, 25, 30 and 35 ◦C) and different nutrients (rice, sesame and date palm). Adult emergence was affected by nutrient, especially temperature, and the performance of insects was determined best in rice and worst in date. Hussain et al. [21] raised *O. surinamensis* adults with six different nutrients: wheat germ, whole wheat flour, rice flour, corn flour, basbousa flour and wheat flour. Mean development times were the longest in corn flour (55.33 days) and rice flour (41.33 days). The shortest time was determined in wheat germ (30.33 days). While the maximum adult emergence was recorded as 69% with wheat germ, this value is minimum (zero) for wheat flour and basbousa. The highest weight loss was determined in wheat germ and corn flour. The growth index was highest in wheat germ and lowest in rice flour. From the results of the chemical analysis, the carbohydrates, total protein, potassium and magnesium contents of the nutrients are directly related to the nutrient preferences of the insects. Mohammadzadeh and Izadi [22] fed *Trogoderma granarium* Everts 1898 (Coleoptera: Dermestidae) with 9 different nutrients (barley, corn, millet, rice, rye, sorghum, triticale, wheat, peanut and walnut) and tested its resistance to cold. Insects reared on triticale had the shortest development time, the highest fecundity and fertility. Survival rates ranged from 40% to 87%, with the lowest values observed in peanuts. The highest larval energy reserve and trehalose level were determined in triticale and the lowest in sorghum. The supercooling point (SCP) of larvae reared on triticale was found to be -20.6 °C, significantly lower than other diets. While the larvae reared with triticale, rye, walnut and peanut withstand -5 and -10°C for 24 h, the mortality rate was 100% in the 20°C/24 h group. These results show that larval nutrient quality can affect the biological and physiological properties, supercooling and cold hardness points of *T. granarium*.

Many insect larvae species show a stable development at optimum temperature. However, changes in optimum temperatures affect the insect's metabolism, reproductive capacity, feeding habits accordingly its distribution [23]. Howe and Currie [23] investigated the effects of temperature on the growth rate, mortality and oviposition of six stored product pests [*Acanthoscelides obtectus* Say 1831, *Callosobruchus maculatus* Fabricius 1775, *C. chinensis* Linnaeus 1758, *C. analis* Fabricius 1775, *C. rhodesianus* Pic 1902 (Coleoptera: Bruchidae) and *Zabrotes subfasciatus* Boheman 1833 (Coleoptera: Chrysomelidae)] and determined the optimum temperatures for each species. They determined that egg hatching in all species was 80% between 17.5 - 30ºC, 70% between 15 and 35ºC, and no eggs were hatched at 40 ºC. The optimum temperature for the fastest development of eggs and larvae was 30 ºC, while the adult emergence was very little at 15 ºC and none at 35 ºC. In addition, the development period and weight of females were higher than males, the heaviest individuals were determined at the lowest temperatures, and the weights decreased with increasing temperature. Omar and Mahmoud [24] determined that egg, larva, pupa and adult cycle for *Callosobruchus chinensis* were inversely proportional to temperature (16, 24 and 32 °C). The longest time required to complete their life cycle at 16 °C as 76.8 days. The optimum temperature for egg, larval and pupal development was determined as 32 °C. Adult survival times were significantly reduced by increasing the temperature from 16°C to 32°C. Also, the data showed that females lived longer than males at all temperatures. It was concluded that temperature significantly affected the pre-oviposition, oviposition and post-oviposition times in *C. chinensis*.

Temperature influences insects in many ways [25-28]. For example, while low temperatures increase larval development time and adult longevity in insects, high temperatures can have the opposite effect [25, 27]. Insects can tolerate temperature changes within certain limits by changing their metabolic activities, regulating their body temperatures or changing their microhabitats, although it varies according to the species [29, 30]. It is known that metabolic activities vary according to age, sex, temperature and nutrient type [27, 31]. The effects of temperature (20, 25 ve 30 ºC) on the resistance of five different bean genotypes (Arc.1S, Arc.1, Arc.2, Arc.4 ve Carioca Pitoco) to *A. obtectus* infestation were investigated. The resistance of Arc.1, Arc.4 and Carioca piteco genotypes decreased with temperature and the invasion rate of *A. obtectus* increased. The most suitable temperature for storage and the highest bean genotype resistance were at 20 ºC [32]. Kpoviessi et al. [33] analyzed vicilin, a-amylase inhibitor, phenols, tannin, carbohydrates, flavonoids and protein in the cowpea genotypes in a study they conducted with *C. maculatus* and 6 genotypes of cowpea seeds. The most resistant genotypes had the highest phenol, carbohydrate and tannin content, while the most susceptible genotypes had the opposite. It was emphasized that there was a relationship between the biochemical content of cowpea seeds and the resistance parameters. Abdel-Hady et al. [34] exposed *Tribolium castaneum* Herbst 1797

(Coleoptera: Tenebrionidae) and *Sitophilus oryzae* Linnaeus 1763 (Coleoptera: Curculionidae), to temperature shock (42 °C for 60, 80, 100 min; 45 °C for 40, 60, 80 min; 48 °C for 15, 30, 45 min; 51 °C for 5, 10, 15 min, 54 °C for 2, 4, 6 min). In both species, life cycle and survival rates were decreased, pupa and recovery time were prolonged, larval period was shortened, food intake was significantly affected and differences in growth rates were detected.

In the study conducted with *C. maculatus* and *C. subinnotatus* Pic 1902 (Coleoptera: Chrysomelidae) oviposition, development and survival rates of these species, which were exposed to three different temperatures (40, 45 and 50 ºC) in different time periods (1, 2, 4 and 6 hours), were investigated [35]. It was determined that the number of eggs laid and adults in both species decreased inversely with temperature and exposure time. Mortality rate was highest at 50 ºC and *C. maculatus* was more sensitive to high temperature than the other species. In addition, there was no development in eggs exposed to 50 ºC for 4 and 6 hours [35].

Generally, two types of behavior are observed in insects depending on the temperature change. First, as the temperature increases, the biological response of the insect increases and lasts until the death limit. Second, an increase in temperature increases the insect's biological response, but after a certain point this response decreases [36]. Johnson and Valero [37] found that when *C. maculatus* eggs, larvae, pupae and adults were exposed to -18 ºC for time intervals (0, 80, 100 and 120 minutes), the highest tolerance to low temperature was in the egg stage and the lowest in adults. It had been reported that the mortality rates of *C. maculatus* and *A. obtectus* increased in direct proportion to the temperature, and *A. obtectus* had a higher tolerance to low temperature [38].

Changes in ambient temperature can alter the dispersal characteristics of insects and migratory routes, resulting in many pest control problems [36]. Stressful situations such as temperature changes or food shortages in the environment of insects play an important role in their physiological and biochemical reactions [16, 27, 28, 39]. When the temperature increase remains within certain limits, enzymatic activity affects positively [40]. However, extreme low or high temperatures directly affect their physiology and have a species-specific response to changing temperatures [25, 27, 28]. These responses may include migrating or changing the geographic location of insects to find places richer in nutrients, more normal temperatures, cannibalism, or early diapause. They regulate their metabolism with these reactions, and develop ecological adaptation by taking physiological and biochemical measures against stressful situations [41]. The amount of nutrients and temperatures that insects need during the larval, pupal and adult developmental stages may vary according to the species. In insects, nutrition [42], metabolism [30, 43], growth rate [28, 35, 43, 44], longevity [26, 45] and reproduction [43, 46] are affected by factors such as temperature and nutrients.

Chandrakantha et al. [42] conducted with different temperatures (20, 25, 30 ve 35 ºC), different cowpea species (*Vigna unguiculata* (Linnaeus) Walp, *Phaseolus radiatus* (Linneaus) R. Wilczek, *Dolichos lab lab* (Linneaus) Sweet and *C. maculatus.* They determined as the temperature increased, the development

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time of the adults was shortened and the oviposition decreased. The type of nutrient was effective in the development of larvae that spent their larval stage in cowpea seeds. Kistler [43] determined that mortality and metabolic rates, growth rates and fecundity of six Coleoptera species [*Stator generalis* Linnaeus 1758, *S. limbatus* Horn 1873, *S. pruininus* Horn 1873, *S. sordidus* Horn 1873 (Coleoptera: Bruchidae), *Mimosestes amicus* Horn 1873 and *Algarobius prosopis* LeConte 1858 (Coleoptera: Chrysomelidae)] increased with temperature (20-50 ºC).

It has been reported that four different temperatures (25, 30, 35 and 40 °C) significantly affect development and oviposition in adults of *C. maculatus* and *C. subinnotatus* [46]. The number of eggs laid by *C. maculatus* adults increased in direct proportion to the temperature, and they laid the most eggs at 35 and 40 °C. *C. subinnotatus* adults laid the most eggs at 30 and 35 °C. Maximum egg development was at 30 °C, and the development time from egg to adult was twice as long at 25 °C [46]. Ferizli et al. [45] determined that *C. maculatus* larvae and eggs could not complete their development when exposed to -18 ºC for 100 minutes or more, and they tolerate other time intervals (20, 40, 60, 80, 100, 120, 140, 160 and 180 m, -18 ºC).

Insects need a certain temperature as they move from one stage to another in their pre-adult developmental stages. Dupuis et al. [44] determined that the mortality rate of *A. obtectus* larvae, pupae and adults was 50% from the 6th day at 0 ºC 1st and 2nd stage larvae live for 4 h at -10 ºC, 6 h for larvae and pupae at other stages, and 16 h at -22 ºC. Sönmez and Koç [47] determined that the longer the storage time at +4 °C, the longer the pupal time and the percentage of deformation of *T. molitor*. Similarly, Sönmez [48] found that the longer the storage time of larvae, the longer the pupal time and the higher the deformation percentage.

Carbohydrates

The types and amounts of basic nutrients needed by insects may vary depending on the species, developmental stages, and physiological conditions such as diapause or migration [49, 50]. Phytophage species belonging to Orthoptera, Coleoptera and Lepidoptera orders generally need equal amounts of protein, carbohydrates and amino acids, while grain pests or storage pests need more carbohydrates [51]. Legume seeds generally contain 20-25% protein, 1-2% fat and 37-50% carbohydrates [52].

Chippendale [53] investigated the effects of different nutrients (starch, dextrin, amylopectin, glycogen, amylose, cellulose, inulin, mono and disaccharides) on the longevity of *S. oryzae*. It was determined the survival rate and longevity of the group fed with polysaccharides were higher than the other group. Stillwell et al. [17] found that when *C. maculatus* larvae were raised in three different legume varieties (*Vigna radiate* (L.) Wilczek, *V. angularis* (Willd.) Ohwi & H.Ohashi, *V. unguiculata* (L.) Walp), the developmental period and the number of eggs laid by the adults varied according to the type of food used. In a study conducted with *S. oryzae* and *S. granarius*, it was determined that the total carbohydrate and lipid amounts in both species increased during the prepupa stage and then decreased [54]. It was stated that the total protein amount increased linearly in the prepupal and adult stages and decreased in the pupal stage in *S. oryzae*, while it increased linearly in all developmental stages in the other species. Allali et al. [55] investigated the fecundities of females in *C. maculatus* reared on different hosts (*Phaseolus vulgaris* L., *Vigna unguiculata* (L.) Walp, *Cicer arietinum* L., *Vicia faba* L., *Pisum sativum* L.). They stated that the fecundity rates and emergence rates in *V. unguiculata*, *C. arietinum* and *P. vulgaris* were higher than other species not included in the nutrient spectrum. The seed surface and husk reduced the percentage of emergence from the seed and the development of surviving adults.

Nutrient is an important environmental factor in the survival of insects. The development, growth and reproduction of insects can be adversely affected and even die in nutrient deficiencies and long-term starvation conditions. However, insects can develop adaptations to nutrient stress, such as diapause, that help increase the amount of lipids or help maintain homeostasis and return the insect back to normal under suitable conditions [41]. Insects may enter diapause as larvae, pupae or adults in stressful situations such as a long winter. It was determined that there was not much difference between trehalose amounts of *Anthonomus grandis* Boheman 1843 (Coleoptera: Curculionidae) adults in diapause compared to non-diapause adults. Although the amount of trehalose was quite low in adults who were fasted for 12-20 hours, it was higher than those in diapause. Glycogen metabolic rate was found to be higher in non-diapause than diapause [56].

Carbohydrates are known to affect insect mortality rates, life cycle and reproductive activities [9, 53]. *A. grandis* fed with a diet containing 2.5% to 10% sucrose and 10% maltose, it was determined that the mortality rates of adults were lower in females fed 10% sucrose and males fed 10% maltose [57]. Glycogen, which is used as an energy reserve in insects, is usually stored in adipose tissue and flight muscles. The qualitative and quantitative composition of the insect's diet significantly affects the storage level of glycogen [58, 59]. When the blood sugar content of insects is low, glycogen is broken down, which raises the blood sugar level. All the sugars in their bodies are converted into glucose to provide ATP, an energy source and metabolic intermediate in living cells [41]. Sharma and Sharma [58] in their study with *C. maculatus* and *Z. subfasciatus*, found that *Z. subfasciatus* adults had more lipids, and that the glycogen amounts of the two species decreased depending on age. It was determined that when *Bruchidius uberatus* Fahraeus 1839 (Coleoptera: Bruchidae), a seed pest, was fed with different nutrients (1% sucrose, only water and control group), the group fed with 1% sucrose had a longer oviposition period than the other groups. The number of eggs laid, the number of hatched eggs, fecundity and longevity were found to be significantly higher [59]. In *Alphitobius diaperinus* Panzer 1797 (Coleoptera: Tenebrionidae), it has been stated that the number of eggs laid by females, development time, fecundity and egg size are affected by the type of nutrient used as a carbohydrate source (barley, maize, rice and white flour) [60].

The reason for high insect infestation in some nutrients may be due to the total carbohydrates, proteins, lipids and minerals contained in the nutrients. These basic nutrients contained in the food can affect the larval development time, the number of eggs they lay, the rate of offspring and the longevity. El-Fouly et al. [61] studied the effects of eight different diets (standard insect rearing diet, wheat germ, oat grains, cumin seeds, maize, chamomile flowers, roselle flowers and fenugreek seeds) on the tobacco beetle *Lasioderma serricorne* Fabricius 1792 (Coleoptera: Ptinidae). The shortest larval period and the highest offspring rate were found in the standard insect rearing diet and wheat germ, while the shortest pupal period was found in the wheat germ. Stathers et al. [2] suggested that *Sitophilus zeamais* Motschulsky 1855 (Coleoptera: Curculionidae) prefers to feed on the endosperm of maize, resulting in greater carbohydrate loss in seeds than protein. In contrast, *Prostephanus truncates* Horn 1878 (Coleoptera: Bostrichidae) depleted the germ and endosperm, causing an extreme reduction in the lipid, protein, iron and zinc grain content of maize. Insect infestation preferences vary with the content of infested nutrients, the type of grain, and the level of infestation.

Proteins

Insects can take the amino acids necessary for their growth and development directly from their food [62]. These amino acids are used in the synthesis of new proteins, enzymes, hormone receptors, neurotransmitters to be synthesized, as well as in activities such as morphogenesis, egg production and maturation of eggs [13, 51, 63]. Proteins and amino acids from food are also used to synthesize egg reserve nutrients materials. Insects fed on nutrients with insufficient protein content limit their reproduction, oviposition and egg hatching.In a study of *Bruchidius dorsalis* Fahraeus 1839 (Coleoptera: Bruchidae) females, it was found that when mated with well-fed males, they lay larger eggs than those mated with undernourished males [19]. With radioactive labeling studies, it has been determined that females in *A. obtectus* obtain the arginine and histidine amino acids they need for oocyte formation and development from the sperm after mating [64]. Velten et al. [65] stated that bean seeds rich in arseline amino acid affect the fecundity of *A. obtectus* females. It was determined that the development time of the larvae was significantly longer than those fed with arselin-free beans, the adults had lower body weights and lay fewer eggs.Yılmaz and Elmalı [66] found that different bean varieties affected the development and reproduction of *A. obtectus*. The larval developmental time, emergence time, longevity, adults weight, and larval mortality rate varied according to the bean variety. A relationship was determined between the duration of the larval period and the protein ratio.

Essential amino acids needed by insects vary according to insect species [51]. The amount of amino acids contained in insects can also vary according to different life stages, sex of the insects and physiological conditions at that time [62, 67]. *C. maculatus* has 20 amino acids in males, 14 in females and eggs, 13 in larvae and 17 in pupae. Alanine, proline, methionine, leucine, threonine and valine in males, alanine, cystine, proline, leucine and valine in females, alanine, proline and leucine in eggs, proline, leucine and valine in larvae, and proline, leucine, phenylalanine and valine in pupae were found.Isoleucine not detected at any developmental stage [67]. Duarte et al. [68] determined that different amino acids were dominant in different developmental stages of *T. castaneum* (larva: valine, pupa: lysine, adult: histidine). They found larvae contained greater amounts of phosphorus, potassium, sulfur and zinc. Some amino acids are needed more in morphogenesis. Although each amino acid varies according to the species, it is used for the formation of different parts of the body. For example, in general, alanine and glycine play an important role in optimal growth, tyrosine in cuticle strength, and tryptophan in the synthesis of pigments [69, 70]. Andersen et al. [69] found that glycine in the adult cuticle of *T. molitor*, and alanine in the larval and pupal cuticle are the dominant amino acids. Dorsal abdomen was rich in apolar amino acids.

Insect species that do not feed in the adult stage or have a short life cycle, meet the necessary energy from the reserves they store in the egg or larval stage. On the other hand, since these energy reserves are not sufficient in species with a long adult life cycle, they usually meet the carbohydrates, proteins and lipids necessary for their vital activities from plant sap, nectar, pollen or host hemolymph [71]. Nectar feeding is common insome species of belonging to Diptera, Lepidoptera, Hymenoptera, and some Coleoptera orders [71, 72]. In some species in Coleoptera order which are storage pests, the energy they provide from the host in the egg or larval stages is very important since the adults are not usually fed. Although they are fed with carbohydrate-rich content, biochemical activities turn them into the substances they need. They must obtain essential amino acids or fatty acids from their hosts.

Changing environmental temperatures effect the amount and types of proteins and amino acids that insects contain. It was determined that *A. diaperinus* females raised at 28 ºC had lower amounts of proline, aspargine and serine amino acids, and higher amounts of tyrosine and lysine than males. The total amount of amino acids was found to be higher in the group exposed to 10 ºC than in the group exposed to 28 ºC [63]. The amount of trehalose, proline, glutamic acid and lysine of *S. oryzae* and *Crystolestes ferrugineus* Stephens 1831 (Coleoptera: Laemophloeidae) was higher in cold hardness (between -10 and -20 °C), and tyrosine was lower [73]. Masoumi et al. [74] fed *C. maculatus* larvae with cowpea seeds treated with proline and trehalose (10, 20, and 40 mmol). They identified potential cryoprotectants effective in supercooling (-18.2 C) and cold hardness (24 h at 0, -5.0, -7.5, -10.0, and -12.5 ◦C). Feeding cowpea seeds treated with proline and trehalose at the larval stage did not affect their amount in adults. *C. maculatus* was not resistant to sub-zero temperatures. Sönmez and Gülel [75] stated that the total carbohydrate, lipid and protein contents of *A. obtectus* adults at 30 °C were higher than those at 20 °C.

Lipids

Most insects need lipids for sexual maturity and egg production [14, 76]. Insects can take lipids through nutrients or synthesize them from proteins and carbohydrates stored in the body through metabolic relationships. Therefore, their amount of carbohydrate and protein content affects the amount of lipids and fatty acids. Lipids consist of fatty acids and have important functions in living organisms [77-79].

They function as a storage and transport form of metabolic fuel in the body's energy production [14]. They are used as a primary energy source during periods of diapause or prolonged migration. Lipids and fattys acids form the structure of cell membranes and the cuticle. Fatty acids are used in the synthesis of pheromones, eicosanoids, waxes and fatty acid-derived hormones [14, 80]. It has been determined by many researchers that the amount and type of fatty acids in insects vary depending on the species, age, sex, developmental stage, tissue, nutrition, physiological conditions and environmental factors [31, 78, 81-83]. Among these environmental factors, temperature is the leading factor affecting their amount of lipids and fatty acids content [77]. It was determined that the total lipid amounts and percentages of *T. molitor* larvae kept in the cold (+4 °C) for 5, 10 and 15 days were higher than the control group, and a decreasing trend was observed kept for 20 days [84]. Sönmez et al. [85] in a study with *A. obtectus*, found that the fatty acid types contained in adult insects remained constant, but their amounts changed depending on age and sex. *A. obtectus* grown at three different temperatures (15, 20 and 30 C°) decreased the total lipid percentage and the total fatty acid increased depending on the temperature increase and sex [86]. Nietupski et al. [87] investigated the effects of surface lipids of different bean varieties on the growth, mortality and oviposition rates of *A. obtectus*. They stated that the rate of oviposition, the rate of dead larvae in the seed and the rate of adults vary according to bean varieties. When bean surface lipids were analyzed, they found wax esters, fatty acids, fatty acid esters, long chain primary alcohols, aldehydes, ketones, squalene and sterols.

In insects, the lipid content is generally higher in the larval stages than in the pupa and adult stages.Triacylglycerols form about 80% of the lipid content, and phospholipids 20% [88, 89]. Insects have high amounts of Omega-3, oleic, linoleic, linolenic acid, and palmitic acid [90-92]. On the other hand, they contain less saturated fatty acids. It has been determined that holometabol insects contain more lipids than proteins in larval stages compared to adults. Similarly, it has been observed in hemimetabol insects. This reason for this larvae store the energy necessary for pupal phase and metabolic activities [91]. Duarte et al. [68] larvae and pupae of *T. castaneum* contained high amounts of SFA (heptadecanoic and stearic acid) and PUFA (α-linolenic and linolenic acids), whereas MUFA was found in very small amounts on the contrary. The highest amount of hypogeic, palmitoleic and oleic acids were detected in adults.

Although the fatty acid types of insects are similar, the dominant fattys acids can be different according to the species. For example, palmitic and oleic acid were determined as dominant fatty acids in *S. oryzae* and *S. Zeamais* [93], oleic and palmitic acid in *C. maculatus* [94], *Dermestes maculatus* De Geer 1774 (Coleoptera: Dermestidae) [95] and *A. grandis* [96], and oleic, palmitic and linoleic acid in *Rhyzopertha dominica* Fabricius 1792 (Coleoptera: Bostrichidae) [97]. Although the number of dominant fatty acids in different species within the same order varies, the fact that oleic and palmitic acids are dominant in all studied species indicates an evolutionary relationship in fatty acid metabolism in insects. Golebiowski et al. [98] found that oleic, linolenic, palmitic, linoleic and stearic acids are present in the cuticle of *A. obtectus*. Oleic and linolenic acid are dominant fatty acids. In studies with *T. molitor*, it was stated that palmitic and stearic acid in the ovaries of females, palmitic, oleic and linoleic acids in adipose tissue [99], palmitic acid in the cuticle [100] were dominant fatty acids. It is known that some of the energy substances needed in the adult stage of insects are met from the nutrient reserves stored in the egg or larval stage [70]. The energy content of newly matured *C. analis* adults was much higher due to the lipids stored in the larval stages and decreased with age [101]. Kurecka et al. [102] found that pupae of *A. diaperinus* contained significantly more protein while larvae more lipid. Females in insects contain higher amounts of lipids for egg production than males. They use most of the lipids for egg reserve nutrition during oogenesis [1, 76, 103]. Thus, they may have higher total lipid percentages than males, although it varies by species. Ximenes et al. [104] with radioactive labeling studies, found fatty acids were used in egg production in *C. maculatus* females, Nwanze et al. [94] found females contain more total lipids and triglycerides than males. It was determined that the total fatty acid amount in *A. grandis* adults was very low in the first four days of adult life and then increased with age [96], while the amount of lipids in the ovaries of *T. molitor* females increased during the first three days of adult life and then decreased [99]. It has been suggested that changes in fatty acid type and amount depending on age, sex and physiological conditions result from the synthesis of eicosanoids or hormones necessary for reproduction and egg laying. Lipids synthesized in adipose tissue during oogenesis are sent to the ovaries to be used in embryogenesis and stored there [14, 80]. It has been shown that oleic acid plays an important role in egg laying in females by detecting that the amount of oleic acid in the ovaries of *T. molitor* females increases during the sexual maturity period [99]. Changes in the amount of oleic acid may be due to the excessive use of oleic acid as a reserve nutrient in the egg in oogenesis or the synthesis of linoleic acid from oleic acid, as suggested by Renobales et al. [105] and Blomquist et al. [106]. Cohen and Levinson [107] suggested that lauric acid increases egg production in *D. maculatus*. Lambremont et al. [108] found that while the amount of monounsaturated fatty acids decreased during reproductive activities in *A. grandis*, the amount of polyunsaturated fatty acids increased.

Fatty acids are used for many different purposes in insects. Palmitoleic acid is used in the synthesis of pheromones in many insects [109, 110]. Meinwald and Eisner [111] and Smith and Grula [112] suggested that caprylic acid is used in defensive secretions in some insects. Cuticular lipids are used for gathering and communication activities in females of some species [98].

Linoleic and linolenic acids and their long-chain metabolites are precursors of eicosanoids, which play an important role in insect physiology. Eicosanoids affect reproduction, cellular immunity and thermoregulation [79, 109, 113]. Insects can convert 18 C polyunsaturated fatty acids to 20 C polyunsaturated fatty acids biochemically [79]. Since eicosanoids, which play an important role in insects, can be synthesized from different fatty acids, these fatty acids can be found in small amounts in insects. Studies have shown that the fatty acids from which eicosanoids are synthesized play an important role as hormones, pheromones and defensive secretions in the immune mechanism and reproduction of insects [81].

Conclusion

In this review study, the physiological effects of temperature and nutrient storage pests are emphasized. In general, carbohydrate, protein and lipid requirements and the effects of these substances on the physiology of insects were evaluated. At the same time, it was evaluated how the temperature affects the protein, carbohydrate and lipid contents of these storage pests. Understanding the physiological and biological relationships in the fight against storage pests will contribute to integrated control methods.

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