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STRESS RESISTANCE: A REVIEW ON DESICCATION RESISTANCE IN DROSOPHILA

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Abstract: Water balance is a challenging process in insects due to their large surface area to volume ratio. Drosophila species adapt various physiological and genetic strategies to overcome the stressful situations such as desiccation and thermal stress. To unravel the mechanism of desiccation resistance in Drosophila species, different studies apply different experimental approaches, which causes variability in the results obtained. A large number of desiccation-related genes have been identified in D. melanogaster which are involved in homeostasis and hygrosensation. The experimental results revealed variations in desiccation resistance within and between the Drosophila species indicating certain relationship between desiccation resistance and other variables. The data obtained on desiccation resistance in Drosophila will help us to predict the response of insects in the changing climatic conditions. Thus, Drosophila species seems to be a perfect biomarker to examine the wide impact of climate change on an organism's genome and its survivability.

Index Terms - insect, desiccation resistance, climate, Drosophila, stress, homeostasis

Introduction:

Water is crucial for life and various complex mechanisms are applied by organisms to avoid water loss. The changes in water availability causes a major stress to organisms thereby influencing their distributions as well as survival (Kellermann et al. ,2018). Desiccation resistance is a phenotypic character which is associated with water content of organisms as well as its rate of water loss (Matzkin et al. , 2007). Drosophila species differ significantly in desiccation resistance which may be correlated to the local climatic conditions (Hoffmann et al., 1999). The wide impact of climate change in recent years is posing a threat to insect's diversity as well as its distribution across the globe (Donnelly, 2018; Hofmann, Fleischmann & Renner, 2018). As climate change has adversely disturbed global water cycles, thus affecting ecosystem and biodiversity.

Nowadays, insects are used as bioindicators for climate change assessment as their response is very clear to the changes in the environment (Lister and Garcia, 2018; Talasova et al. , 2018). Insects are prone to desiccation risk due to their relatively high surface area to volume ratio (Gibbs, 2002b) and they protect themselves against water loss through a variety of mechanisms (Thorat and Nath, 2018). It has been demonstrated that Drosophila may serve as a bioindicator to assess the impacts of climate change on insect genome through observations indicating a latitudinal cline in polymorphism of gene coding for alcohol dehydrogenase (ADH) has shifted during the previous years in response to climate changes in Australia (Umina et al. , 2005).It is advantageous to use Drosophila as a bioindicator as the functional aspect of genes retrieved in field experiments can be tested easily through the powerful genetic tools (Wang et al. , 2021). Thus, it is important to predict the future impacts of climate change on organisms so that we can meet the future challenges of environmental protection and food security.

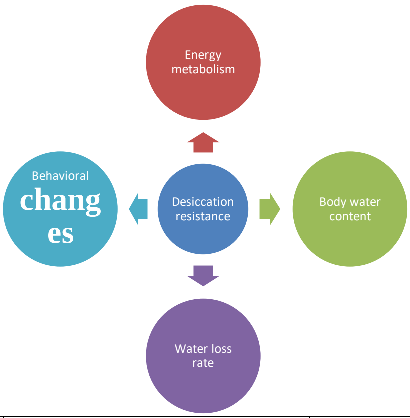
Drosophila melanogaster is a model organism for research purpose at various levels as physiological, ecological and evolutionary levels. Flies of the genus Drosophila are mostly used for studying desiccation resistance mechanisms because of their broad diversity and wide variety of habitats in which they are found ranging from tropical forest to dry deserts (Gibbs, 2002b) and also they are easily reared and manipulated in the laboratory. Drosophila melanogaster has evolved multiple mechanisms to resist water loss through diverse genetic programs. There is involvement of many genes and various genetic networks in desiccation resistance mechanism. The evidences suggest that desiccation resistance level seems to be higher in temperate area population in comparison to tropical ones (Karan et al., 1998). The desiccation resistance in Drosophila is associated with increase in carbohydrate and bulk water content but decrease in cuticular water content and there are also changes in respiratory pattern and behaviour (Bradley et al., 1999). The experimental study has revealed that flies of Drosophila subgenus can better tolerate desiccation stress from the sophophora subgenus at the phylogenetic level (Kellermann et al. , 2012).

Drosophila melanogaster genome was sequenced in 2000(Adams et al. , 2000). Our knowledge regarding evolutionary relationships of Drosophila genus has greatly improved as the genomes of many Drosophila species have been sequenced (Markow, 2015). The billions of SNPs (Single nucleotide polymorphism) recorded in these sequences can also be used for analyzing the various interactions.

This review evaluates findings from various studies on stress-related trait such as desiccation resistance and point out inconsistent results and also paves the way for future perspectives. In this review, our focus mainly relies on desiccation tolerance mechanism in Drosophila. Another future perspective of this review lies as the genome of insects share many genes in common, so the progress and new findings in the genomic data of desiccation resistance in Drosophila melanogaster may also be applied to other insect species.

Mechanisms contributing to desiccation resistance

Drosophila species deploy various physiological adaptations to enhance desiccation resistance which may include behavioural changes, body size, reduction in water loss rates, changes to energy metabolism and tolerance to body water loss (Gibbs & Matzkin, 2001; Gibbs, 2002b).



Features	Organs / Tissues	Proteins / Enzymes
1) Behaviour	Antennae	Obp59a, nan, wtrw, IR25a, IR40a, IR93a
2) Excretory water loss	Hindgut, Malpighian tubules	Capa-1, Capa-2, leucokinin
3) Body water content		Tps1, Treh
4) Energy metabolism		Desi, desat1

Table showing the various proteins and enzymes involved in desiccation resistance mechanism

1) Behaviour

In order to avoid desiccation stress, Drosophila species adapt various behavioural changes. Some species select sites with optimal humidity to avoid arid extremes of environment. The xeric drosophila species had lower metabolic rate and are less active in comparison to the mesic species and thus avoid desiccation thereby reducing their water requirements (Gibbs et al., 2003). D. melanogaster prefer moist locations in its natural habitat as well as in laboratory conditions (Sun et al. , 2018).

In D. melanogaster, the obp59a gene helps in moisture signal detection. This gene encodes a protein named as odorant-binding protein (Obp) which is expressed in the third antennal segment (Sun et al., 2018). In D. melanogaster on the third antennal segment, few water sensing receptors are present which control fly humidity sensing (Liu et al. , 2007; Enjin et al. , 2016). The Nanchung (Nan) and Inactive (Iav) receptors helps in sensing the dry-air whereas Water witch (Wtrw), IR25a, IR40a and IR93a receptors respond to moist air.

2) Body size

Drosophila species vary greatly in their body size. Comparative analysis reveals that larger species are more resistant to desiccation. It was also found that desert species are larger in size in comparison to tropical species (Karan et al. , 1998; Gibbs & Matzkin, 2001). The laboratory selected experiments have revealed contradictory conclusions regarding the association between desiccation resistance and body size (Blows & Hoffman, 1993; Ramniwas et al. , 2013; Rajpurohit et al. , 2016).

3) Energy metabolism

In D. melanogaster desiccation resistance is also influenced by the nutritional content of the food ingested by larvae. It has been demonstrated experimentally that larvae feeding on protein-rich diet were more resistant to desiccation stress in comparison to those larvae feeding on a carbohydrate-rich diet (Andersen et al., 2010). In D. melanogaster, a mysterious gene is also significantly involved in the energy metabolism known as Desiccate (desi). This desi gene is expressed mainly in the epidermis and by suppressing its expression may lead to excessive water loss along with decreased carbohydrate levels (Kawano et al., 2010).

The laboratory experiments revealed that D. melanogaster resistant to desiccation stress have increased storage of glycogen (Gibbs, Chippindale & Rose, 1997; Chippindale et al., 1998; Djawdan et al., 1998). The reason behind this strategy may be due to certain features of glycogen as it binds more water in comparison to lipids (Schmidt-

Nielsen, 1997) and glycogen metabolism also releases water thereby supporting flies during water shortage period (Marron et al. , 2003).

4) Water content and water loss tolerance

Studies revealed that water content remains almost same in the flies of xeric region as well as of mesic region and flies can tolerate upto 45% body water loss before death (Gibbs & Matzkin, 2001). The experiments revealed contradictory results regarding the association between water content and desiccation resistance in flies. In some cases, there was no increase in body water content in the selected Drosophila lines (Blows & Hoffman, 1993; Ramniwas et al. , 2013; Rajpurohit et al. , 2016) while in some other cases, a significant increase in the water content was observed in desiccation selected Drosophila lines (Gibbs et al., 1997; van Herrewege & David, 1997; Chippindale et al., 1998; Folk & Bradley, 2003; Ferveur et al. , 2018).

In D. melanogaster, the body water content was increased in response to desiccation stress. It was due to increase in the haemolymph volume (Folk & Bradley, 2003). A relationship was found between the water content of haemolymph and trehalose concentration (Yoshida et al. , 2016). It was observed that by elimination of trehalose synthase (Tps1) causes a reduction in the haemolymph trehalose concentration and thus haemolymph volume also decreases whereas by eliminating trehalase (Treh), an increase in haemolymph volume was observed.

5) Routes of water loss

In insects, hindgut and Malpighian tubules are involved in excretory water loss, which is estimated to be very low around 5% in Drosophila (Gibbs, Fukuzato & Matzkin, 2003). The diuretic neuropeptides Capability-1 (Capa-1) and Capability-2 (Capa-2) and Leucokinin are involved in this mechanism (Coast et al., 2002).
The respiratory water loss accounts for 25% (Williams, Rose & Bradley, 1997; Williams & Bradley, 1998) while 70% water loss occurs through cuticular evaporation.

Future Trends

- There are 3 transient receptor protein channels present in the third antennal segment of D. melanogaster named as Nanchung, Inactive and Water witch. These channels are responsible for sensing dry and moist air. But, there is no information yet regarding the physiological responses to detection by these protein channels. Thus, in future, research can be carried out to clarify this aspect.
- In D. melanogaster, lipid metabolism is affected by starvation leading to formation of lipid droplets in the oenocytes. This process is carried out by PI3K (Phosphatidylinositide Kinase) in the insulin pathway. There is need to investigate the mechanism by which starvation and insulin signalling affects desiccation tolerance in Drosophila.
- The future work may also focus on finding the correlation between CHC (cuticular hydrocarbon) chain length and desiccation tolerance in Drosophila genus.
- An important gene involved in desiccation resistance is Desiccate (desi), which is expressed in the epidermis of drosophila larvae and protects it from desiccation stress. Future works may focus to identify the biochemical functions and domains of this membrane protein – desi. This will enable us to determine the complex genetic pathway controlling the desiccation resistance.
- Water loss tolerance is also an important factor in regulating desiccation stress but very little information is known till date regarding the molecular and genetic components involved in this mechanism.

Conclusion

Desiccation is a very serious problem for small organisms such as insects. The persistence of water in the surrounding environment of an organism is very important as any alterations in the availability may cause stress to organism thereby influencing its existence, function and position in an ecosystem. Drosophila involves multiple mechanisms such as reducing water-loss rates across the cuticle, increasing their tolerance to water loss and by increasing their water content (Bradley et al., 1999). The logic behind the inter and intra-specific variation in desiccation resistance may be due to the different respiratory patterns adapted between the mesic and xeric species of Drosophila. Thus, desiccation resistance is an additive trait (Mckenzie and Parsons, 1974) which demands more analysis so as to help the organisms survival in the changing climatic conditions of the earth.

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