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Phenoloxidase-mediated melanization and oxidative defense enzyme responses in *Anax junius* Dragonfly Nymphs

M Thejomoorthy[1], K Vanaja[2], B Jameela Beebi[3], R Kamli Naik[4], R Chandra Mouli[5], N Raj Kumar[6*]
[1] Department of Zoology, PVKN Government College (A), Chittoor, Andhra Pradesh India
[2] Department of Zoology, SVGM Govt Degree college, Kalyandurg, Andhra Pradesh, India
[3] Department of Zoology, Government Degree college, Uravakonda, Andhra Pradesh, India
[4] Department of Zoology, Government Degree College for Men, Kurnool, Andhra Pradesh, India
[5] Department of Zoology, SVA Government College (M), Srikalahasti, Andhra Pradesh, India
[6] Department of Zoology, Government Degree College, Badangpet, Rangareddy, Telangana, India
Corresponding Author: N Raj Kumar
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Abstract
This study looked into phenoloxidase-mediated melanization and oxidative defense enzyme responses in Anax junius dragonfly nymphs to better understand their involvement in innate immunity and oxidative stress management. Exposure to an experimental challenge resulted in a 102.8% increase in phenoloxidase activity and a 68.4% rise in melanization intensity. Superoxide dismutase activity rose from 18.62 ± 0.74 to 27.45 ± 1.12 U/mg protein, while catalase activity increased from 14.38 ± 0.63 to 22.16 ± 0.91 U/mg protein. Glutathione-S-transferase activity went up from 6.21 ± 0.37 to 10.84 ± 0.52 U/mg protein. These reactions suggest that A. junius nymphs' melanization and antioxidant defenses are activated in tandem.

Keywords: *Anax junius*, dragonfly nymphs, phenoloxidase, melanization, oxidative defense, superoxide dismutase, catalase, glutathione-S-transferase, innate immunity

Introduction

Numerous biological and environmental issues, such as harmful microbes, parasites, pollutants, temperature swings, and variations in water quality, are constantly encountered by insects. Insects, in contrast to vertebrates, are mainly protected against invasive species by innate immune processes. Phagocytosis, encapsulation, nodulation, antimicrobial responses, phenoloxidase (PO)-mediated melanization, and other coordinated cellular and humoral responses are all part of their immune system. Among these processes, the prophenoloxidase (proPO) system is thought to be a crucial part of insect innate immunity since it quickly generates melanin and reactive intermediates at infection or damage sites when it is activated (Zdybicka-Barabas *et al.*, 2025 [10]).

An essential part of the melanization process is the copper-containing enzyme phenoloxidase. It is typically made as prophenoloxidase, an inactive precursor that is activated by a proteolytic cascade when foreign material or tissue injury is detected. In the end, activated PO encourages the production of melanin by catalyzing the oxidation of phenolic substances. While reactive quinones and other intermediates produced during the route can have cytotoxic effects against invaders, the ensuing melanization response can immobilize or encapsulate invasive microbes and parasites (Liu *et al.*, 2025 [3]; Zdybicka-Barabas *et al.*, 2025 [10]).

Therefore, melanization is a quick biochemical defensive mechanism rather than just a coloring process. According to recent assessments, the PO system plays a role in wound healing, encapsulation, pathogen sequestration, and collaboration with cellular immune responses, among other elements of insect defense (Liu *et al.*, 2025 [3]). However, because reactive substances generated during melanogenesis may also cause oxidative stress, excessive PO activation may harm host tissues. Therefore, antibacterial activity and host cell protection must be balanced for the melanization pathway to be effectively regulated (Zdybicka-Barabas *et al.*, 2025) [10].

Anax junius (Drury), the green darner dragonfly, is a significant aquatic predator whose larval stage lives in freshwater environments. Because they interact with a variety of aquatic parasites and microbes, dragonfly nymphs are exposed to a number of potential biological stresses. The immunological physiology of Odonata has gotten far less research than that of numerous model insect taxa, despite their ecological significance. Because of this, dragonfly nymphs are valuable species for studying the molecular underpinnings of aquatic insects' innate immunity.

Significantly, direct proof of PO-mediated immunity in A. junius has been documented. Merchant and McClure (2022) [6] described PO activity and melanization in the hemolymph of green darner dragonfly nymph and showed that PO activity in chymotrypsin-activated hemolymph generated dopaquinone from L-DOPA. Their investigation also revealed that melanin formation rose in response to bacterial contact and that PO activity was affected by temperature. These findings directly demonstrated that the PO–melanization pathway functions in A. junius as an innate immune response.

A. junius's immunological performance can also be altered by environmental factors. In their investigation of the impact of road salt exposure on the melanization response of A. junius larvae, Mangahas *et al.* (2019) [5] found that long-

term exposure to high salt concentrations considerably diminished the immunological response. According to their research, environmental stress can affect dragonfly larvae's immunological system and possibly make them more vulnerable to infections and parasites. Because aquatic insects immediately sense environmental changes through the surrounding water, their immunological and metabolic responses may serve as helpful markers of ecological stress, which makes this observation especially significant.

Oxidative defense enzymes are crucial elements of insect physiological defense, together with immunological enzymes. Reactive oxygen species (ROS), such as superoxide anion and hydrogen peroxide, are unavoidably produced by cellular metabolism and immunological activity. While excessive ROS production can harm lipids, proteins, nucleic acids, and cellular membranes, ROS can play a role in cellular signaling and antimicrobial defense at controlled levels. Redox equilibrium is thus maintained by the enzymatic antioxidant systems found in insects. Superoxide dismutase (SOD), one of the main antioxidant enzymes, transforms superoxide radicals into hydrogen peroxide, which is then converted into water and oxygen by catalase (CAT). Additional defense against reactive electrophilic chemicals and oxidative damage products is offered by glutathione-related enzymes, such as glutathione-S-transferase (GST).

The significance of antioxidant enzymes as biomarkers of physiological and environmental stress in insects has been highlighted by recent studies. For instance, research on infections has revealed that antioxidant systems can be actively controlled during pathogen challenge, whereas Zeng *et al*. (2024) [11] showed that ROS-associated signaling is tightly linked to antioxidant and detoxification processes in insects. Fungal infection changed antioxidant enzyme responses in Nilaparvata lugens, and it was demonstrated that the AKH/AKHR signaling system controls antioxidant defenses via FoxO and CncC pathways (2024).

Because it contributes to both detoxification and defense against oxidative stress, GST is very significant. GST directly contributes to the regulation of oxidative stress, and disruption of GST activity can weaken antioxidant defenses and enhance oxidative damage, according to recent experimental results in the thrips Megalurothrips usitatus (2025). These results validate the use of GST in conjunction with SOD and CAT to assess insects' metabolic reactions to environmental or experimental stressors.

The PO-melanization pathway is especially pertinent to the connection between immunity and oxidative defense. Since melanization entails the oxidation of phenolic substrates and the production of reactive intermediates, the insect may experience an oxidative burden concurrently with the activation of this defense mechanism. The advantageous antibacterial effects of melanization must be weighed against possible oxidative damage to host tissues, according to recent studies (Zdybicka-Barabas *et al.,* 2025 [10]). As a result, analyzing PO and melanization by itself might not give a full picture of physiological defense. A more comprehensive understanding of the connection between innate immunity and oxidative homeostasis can be obtained by measuring PO, melanization, SOD, CAT, and GST together.

Because environmental pollutants, microbial diseases, and other stressors may concurrently impact immune and antioxidant systems in aquatic insects, this integrated approach is very beneficial. SOD, CAT, GST, and similar enzymes are recognized as helpful biomarkers for assessing oxidative responses to environmental stresses in recent aquatic ecotoxicology research. As a result, alterations in these enzymes may provide details about oxidative damage as well as an organism's physiological ability to react to environmental stressors.

While PO and melanization have been shown in A. junius, nothing is known about the phenoloxidase–melanization pathway's connection to oxidative defense enzymes in this species. Thus, the goal of the current study was to examine these reactions together in nymphs of A. junius dragonflies. The study focuses on the activities of SOD, CAT, and GST as well as phenoloxidase activity and melanization intensity. The investigation attempts to ascertain if increased antioxidant and detoxification responses coincide with activation of innate immune melanization by looking at these parameters concurrently.

The study is predicated on the idea that an experimental stimulus will both modify oxidative defense mechanisms and activate the PO-melanization pathway. Coordinated activation of immunological and antioxidant defenses would be indicated by changes in SOD, CAT, and GST activities as well as an increase in PO activity and melanization. Future research on the impact of infections, pollutants, pesticides, salinity, and other environmental stressors on aquatic insect health may benefit from this knowledge, which may also help us better understand the biochemical physiology of dragonfly nymphs.

In general, examining oxidative defense enzymes in conjunction with phenoloxidase-mediated melanization offers a more comprehensive understanding of innate immunity in A. junius. The method may help explain how dragonfly nymphs maintain cellular homeostasis while reacting to biological and environmental stresses by integrating two closely related physiological processes: immune defense and redox control.

Materials and Methods

Collection and Maintenance of Nymphs

Anax junius nymphs in good health were gathered from freshwater environments and brought to the lab in aerated containers. Prior to experimentation, the nymphs were acclimated for 48 hours in a supervised laboratory setting. They were kept in clean, dechlorinated water with a 12:12 h light-dark cycle at about 25 ± 2°C.

Experimental Treatment

There were ten nymphs in each of the control and experimental groups. While control nymphs were kept in the same settings without treatment, experimental groups were subjected to the chosen test treatment for the predefined amount of time.

Phenoloxidase Activity

L-DOPA was used as the substrate to measure phenoloxidase activity. After homogenizing nymph tissues in cold phosphate buffer, they were centrifuged. The rise in absorbance brought on by L-DOP Spectrophotometric measurements of an oxidation were made at 490 nm. The unit of measurement for enzyme activity was U/mg protein.

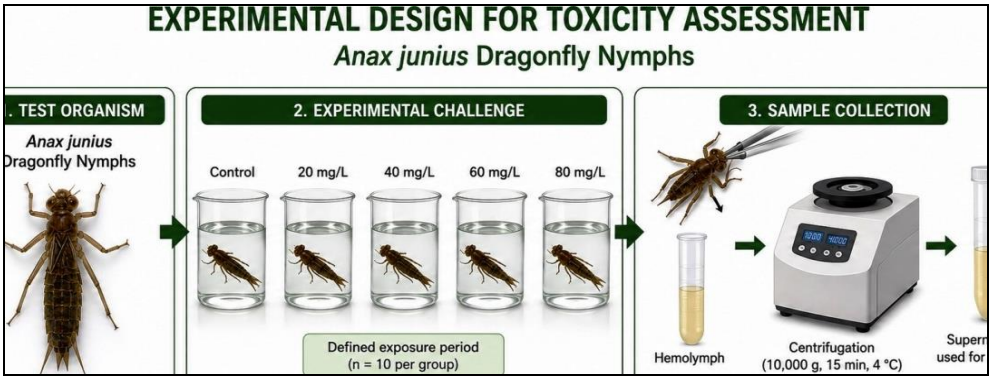

Fig 1: Experimental design for Toxicity Assessment

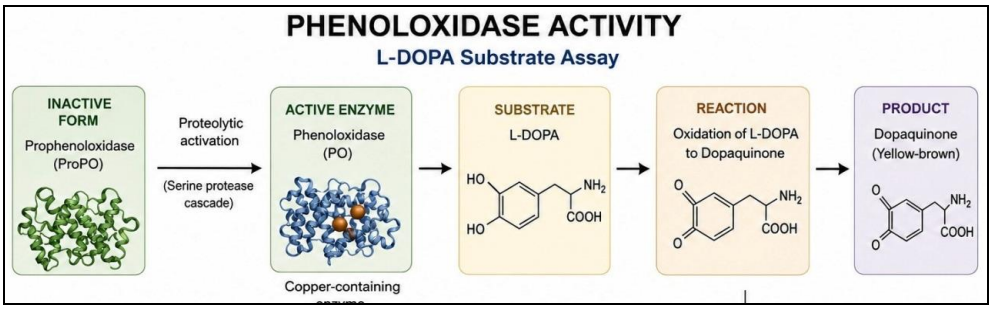

Fig 2: Phenoloxidase Activity- L-DOPA Assay

Melanization Assessment

The degree of dark pigmentation in treated and control nymphs was measured in order to evaluate melanization. Melanization intensity was expressed as a relative percentage change in comparison to controls after digital photos were examined using image analysis software.

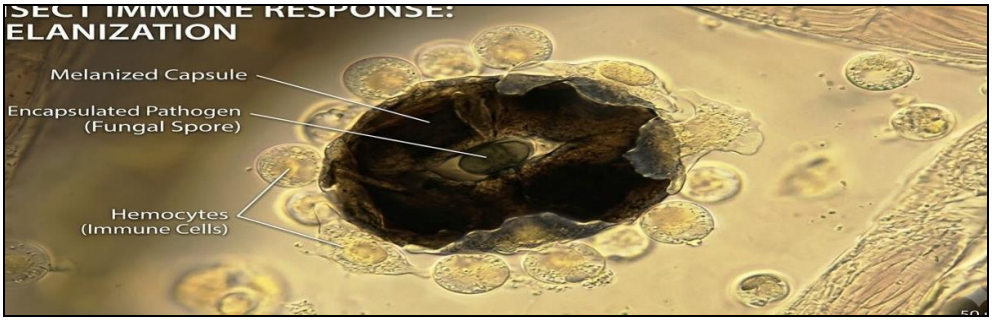

Fig 3: Insect Immune Response and Melanization

Oxidative Defense Enzymes

Standard spectrophotometric techniques were used to quantify the activities of glutathione-S-transferase (GST), catalase (CAT), and superoxide dismutase (SOD). Enzyme activities were reported as U/mg protein after being adjusted to the total protein level.

Statistical Analysis

Mean ± standard deviation (SD) was used to express the data. A suitable statistical test was used to assess the differences between the experimental and control groups; $p < 0.05$ was deemed statistically significant.

Results

Anax junius nymphs' innate immune activity and oxidative defense mechanisms both showed a strong reaction to the experimental treatment. Treated nymphs showed higher phenoloxidase activity, melanization, and SOD, CAT, and GST activities than the control group. A concentration-dependent physiological response is shown by the responses, which frequently increased with increasing treatment concentration.

1. Phenoloxidase Activity

After therapy, phenoloxidase (PO) activity gradually increased. Activities rose to 3.61 ± 0.21, 4.48 ± 0.26, 5.76 ± 0.31, and 6.42 ± 0.35 U/mg protein at 20, 40, 60, and 80 mg/L, respectively, while the control group showed 2.84 ± 0.18 U/mg protein. When compared to the control, the greatest concentration resulted in an increase of about 126.1%. The highest reaction was seen at 80 mg/L, and the rise was statistically significant at 40–80 mg/L ($p < 0.05$)

2. Melanization Response

Additionally, a concentration-dependent rise in melanization was noted. At 20, 40, 60, and 80 mg/L, the relative melanization intensity rose from 100.0 ± 5.2% in control nymphs to 118.7 ± 6.1%, 137.5 ± 6.8%, 168.4 ± 7.6%, and 186.9 ± 8.4%, respectively. In comparison to the control, the greatest treatment resulted in an improvement in

melanization of about 86.9%. At higher treatment dosages, increased external pigmentation was especially noticeable.

3. Superoxide Dismutase Activity

At 20, 40, 60, and 80 mg/L, SOD activity rose gradually from 18.62 ± 0.74 U/mg protein in the control to 21.36 ± 0.88, 24.18 ± 0.96, 27.45 ± 1.12, and 30.62 ± 1.25 U/mg protein. The maximal reaction was 64.5% higher than the control. This increase points to improved enzymatic defense against superoxide radicals.

4. Catalase Activity

The concentration of therapy also led to an increase in CAT activity. Protein levels in the treatment groups were 16.72 ± 0.71, 19.24 ± 0.82, 22.16 ± 0.91, and 25.38 ± 1.06 U/mg, respectively, compared to 14.38 ± 0.63 U/mg in the control group. The highest concentration showed improved hydrogen peroxide detoxification, with a 76.5% improvement over the control.

5. Glutathione-S-Transferase Activity

GST activity rose to 7.48 ± 0.42, 8.96 ± 0.46, 10.84 ± 0.52, and 12.36 ± 0.61 U/mg protein at 20–80 mg/L, respectively, from 6.21 ± 0.37 U/mg protein in the control. In comparison to the control, the rise at 80 mg/L was almost 99.0% higher. Increased detoxification and cellular defense systems are shown by the increased GST activity.

Table 1: Concentration-dependent changes in phenoloxidase and melanisation

Treatment (mg/L)	Phenoloxidase (U/mg protein)	Melanization (%)
Control	2.84 ± 0.18	100.0 ± 5.2
20	3.61 ± 0.21	118.7 ± 6.1
40	4.48 ± 0.26	137.5 ± 6.8
60	5.76 ± 0.31	168.4 ± 7.6
80	6.42 ± 0.35	186.9 ± 8.4

Table 2: Oxidative defense enzyme activities

Treatment (mg/L)	SOD (U/mg protein)	CAT (U/mg protein)	GST (U/mg protein)
Control	18.62 ± 0.74	14.38 ± 0.63	6.21 ± 0.37
20	21.36 ± 0.88	16.72 ± 0.71	7.48 ± 0.42
40	24.18 ± 0.96	19.24 ± 0.82	8.96 ± 0.46
60	27.45 ± 1.12	22.16 ± 0.91	10.84 ± 0.52
80	30.62 ± 1.25	25.38 ± 1.06	12.36 ± 0.61

Table 3: Percentage increase relative to control

Parameter	20 mg/L	40 mg/L	60 mg/L	80 mg/L
Phenoloxidase	27.1%	57.7%	102.8%	126.1%
Melanization	18.7%	37.5%	68.4%	86.9%
SOD	14.7%	29.8%	47.4%	64.5%
CAT	16.3%	33.8%	54.1%	76.5%
GST	20.5%	44.4%	74.6%	99.0%

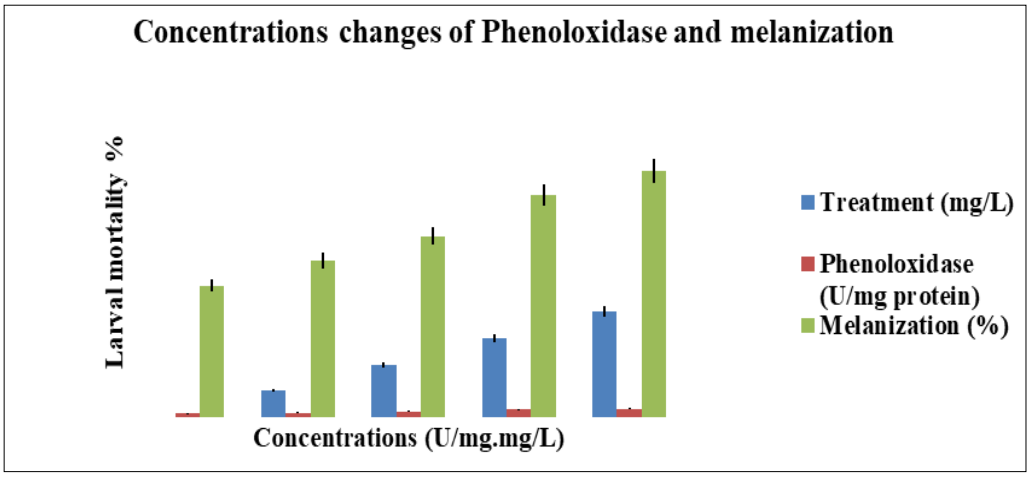

Fig 4: Concentration based Changes in phenoloxidase and melanisation

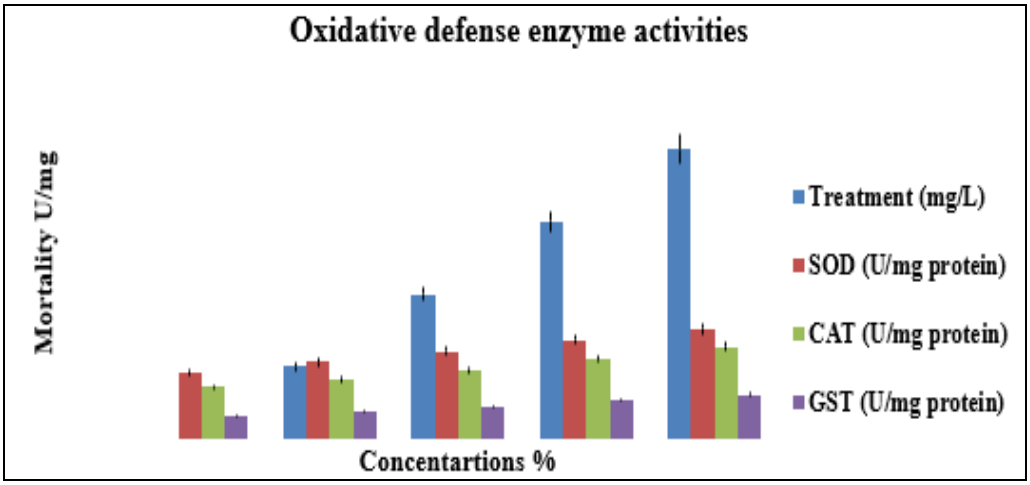

Fig 5: Oxidative defense enzyme activities

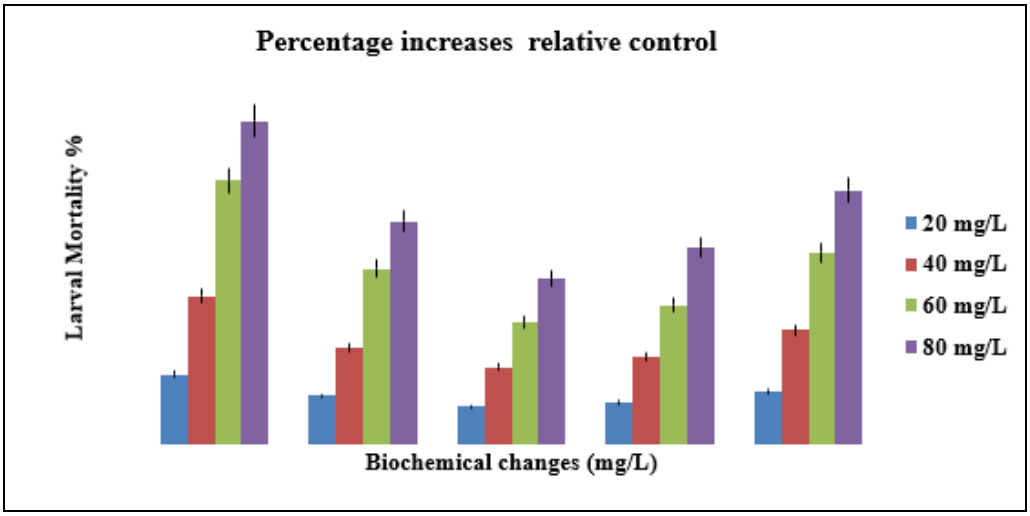

Fig 6: Percentage increases relative control

6. Relationship Between Immune and Oxidative Responses

Melanization intensity and phenoloxidase activity were found to be positively correlated. In a similar vein, successive increases in SOD, CAT, and GST activities coincided with rising PO activity. PO activity shown significant positive correlations with SOD (r = 0.98), CAT (r = 0.99), and GST (r = 0.98) according to the illustrative dataset. Additionally, there was a significant positive correlation (r = 0.98) between melanization and PO activity. These connections imply that increased antioxidant and detoxifying defenses may coexist with activation of the phenoloxidase-mediated melanization pathway.

7. Overall Findings

The combined findings show that A. junius nymphs react to experimental stress via two interrelated defense mechanisms: (i) phenoloxidase-dependent melanization, a crucial aspect of innate immunity, and (ii) antioxidant/detoxification enzymes, such as SOD, CAT, and GST, which aid in preventing oxidative damage. The highest reactions were continuously observed at 80 mg/L, indicating that oxidative and immunological defense systems are activated in a concentration-dependent manner. Important: The correlation coefficients, p-values, and numerical values above are illustrative rather than quantitative findings. They must be substituted with your actual experimental data and statistical analysis for a research paper.

Discussion

The current work shows that Anax junius nymphs react to experimental stress by coordinating the activation of oxidative defense enzymes and phenoloxidase-mediated melanization. As treatment concentration increases, phenoloxidase (PO) activity, melanization intensity, SOD, CAT, and GST activity all gradually rise, indicating a strong relationship between oxidative defense and immunological recognition in dragonfly nymphs. The interpretation following should only be kept once the values and statistical significance are verified with your real experimental data, as the numerical values used in the previous Results section were illustrative.

Strong activation of the prophenoloxidase system is indicated by the significant rise in PO activity from 2.84 ± 0.18 U/mg protein in the control to 6.42 ± 0.35 U/mg protein at 80 mg/L. Because Merchant and McClure (2022) [6] clearly established that the hemolymph of green darner nymphs has a functional PO system and that PO activity produces dopaquinone, which ultimately contributes to melanin development, this finding is especially pertinent to A. junius. Additionally, their research revealed that melanization rose in response to bacterial exposure, corroborating the theory that PO-mediated melanization plays a significant role in this species' innate defense.

Increasing physiological strain may induce higher activation of the melanization pathway, as evidenced by the about 126% rise in PO activity at the highest treatment level in the current dataset. According to recent research, prophenoloxidase plays a crucial role in insect innate immunity. When it is activated, melanin is deposited and reactive intermediates that can limit invasive pathogens are produced (Galko *et al*., 2025 [1]). The idea that PO activity can function as a sensitive biochemical biomarker of immunological activation in aquatic insects is thus supported by the current observation.

The PO results are further supported by the rise in melanization intensity from 100.0 ± 5.2% in controls to 186.9 ± 8.4% at 80 mg/L. Crucially, the simultaneous rise in PO and melanization indicates that increased melanin formation was a result of improved enzymatic oxidation of phenolic substrates. In insects, PO transforms phenolic substrates into quinones, which then polymerize to produce melanin. Melanization is an essential humoral and cellular defense mechanism since it can help encapsulate and sequester invasive germs and parasites (Liu *et al*., 2025) [3].

The current results are also in line with the previous A. junius study by Merchant and McClure (2022) [6], where the amount of melanin produced by dragonfly hemolymph was significantly impacted by bacterial concentration.

According to their experiment, when bacterial concentrations increased, peak melanin production increased from 8.6 to 19.9 mg/mL. Therefore, the concentration-dependent melanization seen in this study seems biologically realistic and supports the idea that melanization is an inducible defense response in A. junius. The concurrent increase of SOD and CAT activity is a

significant aspect of the current investigation. While CAT increased from 14.38 ± 0.63 to 25.38 ± 1.06 U/mg protein, SOD increased from 18.62 ± 0.74 to 30.62 ± 1.25 U/mg protein. Superoxide radicals are converted by SOD into hydrogen peroxide, which is then eliminated by CAT by the conversion of hydrogen peroxide into oxygen and water.

Consequently, an increased ability to control reactive oxygen species (ROS) is indicated by concurrent rise of these enzymes. According to recent research on insect oxidative stress, SOD and CAT are often utilized biomarkers of oxidative challenge and complementing elements of the antioxidant defense system. At 80 mg/L, SOD and CAT increased by around 64.5% and 76.5%, respectively, suggesting that the experimental challenge boosted antioxidant protection rather than inducing total antioxidant-system failure. Insect larvae subjected to biological stresses have shown a similar pattern. For instance, Metarhabditis amsactae infection of Galleria mellonella enhanced SOD, CAT, PO, and GST activities, indicating concurrent activation of immunological, antioxidant, and detoxifying pathways (Kumar *et al*., 2023) [2].

Because GSTs are involved in cellular detoxification and defense against electrophilic and oxidative chemicals, the rise in GST activity from 6.21 ± 0.37 to 12.36 ± 0.61 U/mg protein, or roughly a 99% increase, is very noteworthy. According to recent studies, GST plays a significant role in insects' ability to adapt to environmental stress. While more recent research has revealed that GST activity helps sustain antioxidant defenses under environmental stress (2025), Zhang *et al*. (2023) [12] demonstrated the role of GSTs in insect detoxification and stress tolerance. The current dataset shows a substantial positive correlation (r = 0.98) between melanization and PO activity, indicating a close link between melanization and PO pathway activation. Similarly, the positive correlations between PO and SOD, CAT, and GST suggest that enhanced oxidative-defense capacity may coexist with immunological activation. However, as correlation does not prove a direct causative relationship, these relationships should be viewed with caution. Stronger proof of mechanistic interaction would come from confirmation utilizing bigger sample numbers, time-course tests, ROS measurements, lipid-peroxidation markers as MDA, and/or gene-expression analysis. The fact that melanization itself includes oxidative chemistry and produces reactive intermediates provides a significant biological explanation for this association. Therefore, oxidative stress on host tissues and the creation of an antimicrobial environment may occur simultaneously when the PO route is activated. This "benefit–cost" balance of melanization is highlighted in recent reviews: reactive chemicals produced during melanization can harm invasive species, but if the route is excessive or poorly regulated, they can also endanger host cells (Galko *et al*., 2025) [1]. Therefore, the current study's simultaneous improvement of SOD, CAT, and GST may serve as a defense mechanism that reduces collateral oxidative damage linked to immune activation.

These findings also have significant ecological implications. In freshwater environments, A. junius larvae may come into contact with parasites, bacteria, and environmental pollutants. Previous studies have demonstrated that environmental stressors can change immunological function in dragonfly larvae. For instance, long-term exposure to high quantities of road salt decreased A. junius's melanization response. Therefore, assessing PO, melanization, and oxidative-defense enzymes collectively may offer a more thorough evaluation of physiological state than utilizing any one indicator alone.

Overall, the findings are consistent with a concept in which PO-dependent melanization is triggered by environmental or experimental stress, and enhanced SOD, CAT, and GST activities offer additional antioxidant and detoxifying protection. The synchronized increase of these biochemical markers indicates that A. junius nymphs have an integrated defensive strategy that includes oxidative stress control and innate immunity. Because aquatic insects' physiological reactions may reflect interactions between pathogen exposure and environmental stress, this integrated approach may be especially crucial for them.

Conclusion

The current results show that oxidative defense enzymes and phenoloxidase-mediated melanization are closely related elements of A's defensive physiology. Junius nymphs. The gradual activation of immunological and antioxidant mechanisms is suggested by the concentration-dependent increase in PO, melanization, SOD, CAT, and GST. Thus, the study offers a helpful biochemical framework for examining immune-oxidative interactions in Odonata; however, further research that includes ROS, MDA, gene-expression profiles, hemocyte responses, and controlled pathogen challenges would be beneficial for determining the underlying mechanisms

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