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Effects of Temperature on Light Emissions of Fireflies: A Brief Review

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Abstract

The firefly could be considered as an optical signalling system: males of this insect flash in search of females, and females respond with precisely timed flashes of their own. The chemical reaction that produces this light is instantaneously affected by temperature, and the effect is manifested in the emitted pulses. From the nature of the pulses, conclusions could be drawn and hypotheses put forward regarding the speed of the chemiluminescence reaction. The emitted light and flashes at very high and very low temperatures also give an indication of the change in the structure of the enzyme luciferase that catalyses the reaction. In this review, studies carried out on firefly emissions at different temperatures and comparisons with those under static magnetic and electric fields are presented.

Keywords: *Firefly bioluminescence, pulse broadening, pulse narrowing, reaction speed, peak shift*

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1. Analysis and Results :

The light of the firefly has been a topic of interest for scientists for almost a century. This light is the outcome of a very efficient chemical reaction [Ando et al., 2008], called chemiluminescence reaction, which is the main reason for this interest. In this light-producing reaction, triggered by molecular oxygen, luciferin is the substrate, and the enzyme luciferase acts as a catalyst in the

presence of Mg^{2+} and adenosine triphosphate (ATP).An unstable dioxetanone intermediate is generated, which decomposes to form an electronically excited oxyluciferin species. While decaying to the ground state, the excited oxyluciferin emits light in the visible region.

In vivo firefly bioluminescence has been found to be instantaneously affected by temperature. Low temperature slows down the reaction and as a result, the pulses become long, while high temperature speeds up the reaction and the quick ending makes the pulses short. For the Indian species of firefly *Absconditaperplexa* (changed nomenclature from *Luciolapraeusta*), a decrease of approximately 3 ms for each °C increase in temperature was observed in the range of 20 °C – 40 °C [Sharma et al 2014]. Figure 1 presents the pulse-widths at different temperatures. This means that the speed of the bioluminescence reaction increases with an increase in temperature, and this increase is substantially linear, especially in the normal flashing range of 25°C – 35 °C.

At temperatures lower than about 20°C, it was observed that the ordered nature of the flashes is lost, and compound or combination flashes manifest along with the simple ones [Sharma et al., 2016]. Even in the case of simple flashes, the pulse width increased abnormally with considerable deviation. Simple flashes of 97 (±0.29)ms at 30 °C became 261 (± 37) ms, 296 (±71) ms and 470 (±93) ms at 18 °C, 16 °C and 14 °C, respectively. At 12 °C, only one flash of duration 1 s could be recorded in that study. Hence, it may be inferred that the rate of the luciferase-luciferin reaction slows down considerably in a non-uniform and highly variable manner at such low temperatures. It is therefore clear that low temperatures affect the rate of flow of oxygen to the photocytes, where luciferin and luciferase are housed. The oxygen flow stops momentarily after the excitation of a group of luciferin molecules, and then continues and excites the remaining molecules or the remaining ‘group’. It was hypothesized that the firefly flashes are shaped by neural impulses generated in the brain that eventually impinge on the lantern tissue.

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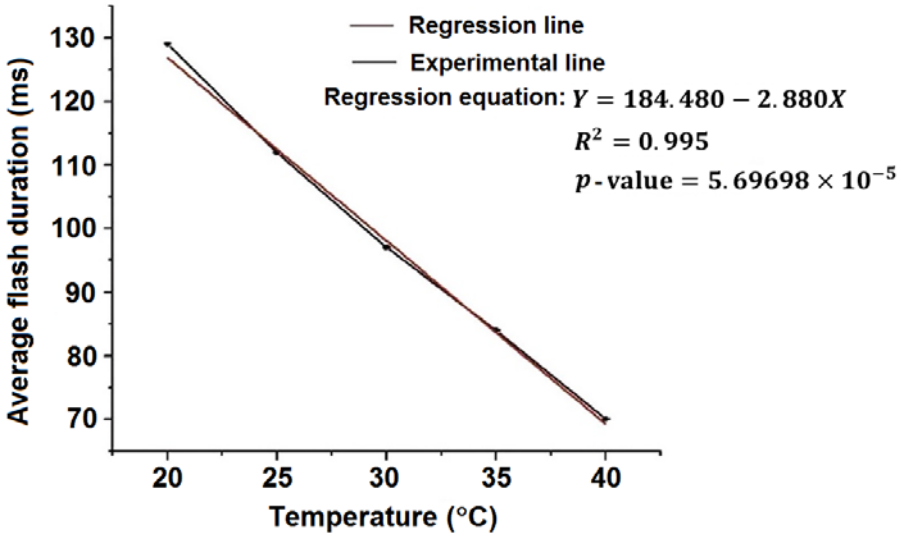


Figure 1. Firefly-flash duration at temperatures 20°C – 40 °C [Sharma et al., 2014]. The duration varies approximately linearly with temperature, especially from 25 °C upwards.

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The neurotransmitter responsible for the induction of luminescence in the firefly lantern is widely believed to be octopamine. The flashes recorded at low temperatures imply that the neuro-transmitter octopamine gets affected at low temperatures.

The broad overlapped flashes at low temperatures could be compared to those obtained from fireflies placed in a strong static magnetic field [Gohain Baruah et al., 2012], shown in Figure 2. It was earlier reported that high-intensity static magnetic fields decrease the skin temperature of an animal [Ichioka, et al., 2000] the mechanism suggested was associated with magnetically induced movement of water vapour at the skin surface [Ichioka et al., 2003]. The strong static magnetic field possibly affected the body temperature of the firefly. The broadest flash of duration 400 ms was recorded for the firefly *A. perplexa* when placed under the 10 T field for a sufficiently long time. Therefore, low temperatures appear to have nearly similar effects on the firefly-flashes as that of the strong static magnetic field.

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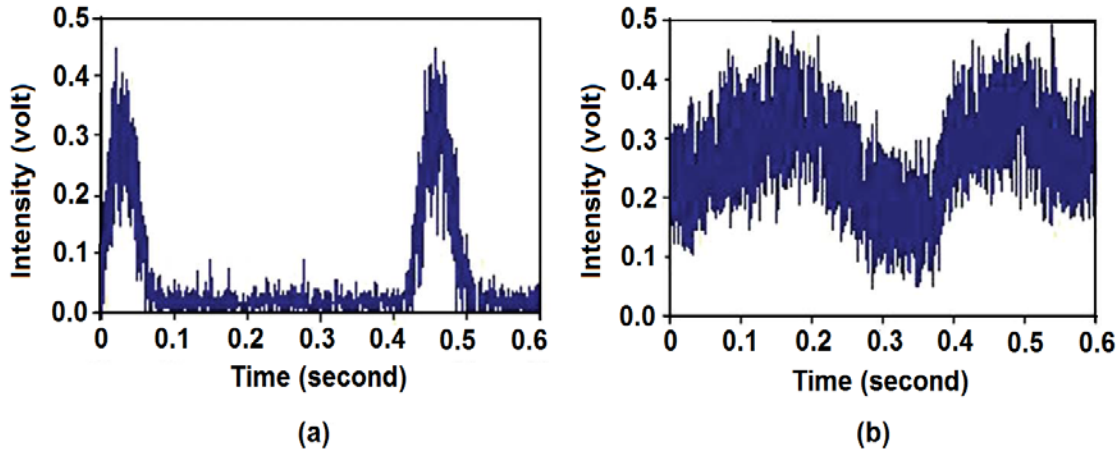


Figure 2. Flashes from the firefly *Absconditaperplexa* in normal and under a strong static magnetic field [Gohain Barua et al., 2012]. (a) At 25 °C, the flashes are of duration approximately 100 ms., (b) Under the superconducting magnet of field strength 10 T, the flashing becomes rapid, and the pulses occasionally come together to form big flashes of duration (in this case) 400 ms.

At such low temperatures, a simple flash frequently got split into two and sometimes three [Goswami et al., 2019]. It is well known that the emitter molecule oxyluciferin has six luminescent forms, out of which three are luminescent. Therefore, it was concluded that the three peaks in a flash represent the three luminescent forms of oxyluciferin, and their lifetimes of a few tens of, or a hundred-odd, milliseconds point towards *phosphorescence* as the process involved in the in vivo firefly bioluminescence emission. There had been an ingrained view that the excited oxyluciferin molecule decays via a fluorescence pathway. The reason for that view was the nanosecond lifetimes obtained for different analogs of oxyluciferin. But no chemical reaction takes place in typical luminescence — excitation is done externally; hence the conclusion that the chemiluminescence reaction in the firefly makes the situation favourable for intersystem crossing in the excited state.

A set of nonlinear differential equations was proposed somewhat recently to represent the cyclic creation and consumption of the intermediate compounds, notably the inhibitory and stimulatory roles of oxygen and nitric oxide [Saikia and Bora, 2020]. A time-delay differential equation was introduced to account for physiological transport and chemical relaxation times. This time-delay leads to Hopf bifurcations, reproducing the multi-peak (bi-modal or tri-modal) flash shapes observed in *A. perplexa* and *A. circumdata* fireflies in cold temperatures. In nonlinear dynamics, the

frequency and shape of the flashes are heavily dependent on control parameters like the rate of oxygen diffusion. This model shows that as ambient temperature drops, the bifurcation parameter (representing metabolic rate and enzyme activity) pushes the system into different regimes ¾ shifting from single sharp flashes to complex oscillatory delayed patterns.

At very high and very low temperatures, the wavelength peak shifted towards red and blue, respectively, indicating denaturation of the luciferase [Rabha et al., 2017; Rabha et al., 2021].The temperatures of probable thermal denaturation for the easily available species *Absconditaperplexa* was determined as 42 °C for its females and 41.5 °C for males, and 34 °C for *Sclerotiasubstraiata* males [Rabha et al., 2021]. At the temperature of probable thermal denaturation, the pulse width became the minimum, and thereafter it increases sharply for small increase in temperature. Temperatures of probable cold denaturation for *A. perplexa* males and females were found as 11.5°C-11.0°C and 16.5°C-15.0°C [Borah et al., 2023]; for *S. Substriata* males this temperature was 10.5°C-9.0°C [Rabha et al., 2021].From the temperature of probable cold denaturation also, the flash-duration increased noticeably for small decrease in temperature. The wavelength peak-shift and flash-duration were reversible in the case of cold denaturation and irreversible for hot denaturation. Fireflies starting to flash within half an hour of sunset are categorised as early-starting or dusk-active, while those begin flashing after half an hour of sunset are clubbed as late-starting or dark-active [Lall et al., 1980]. The temperature optimum of 42 °C for *A. perplexa* could be cited as the reason for this species being early-starting or dusk-active; on the other hand, the temperature of 34 °C for *S. substriata* ensures that it is late-starting or dark-active [Rabha et al., 2021] Also, because of these two temperature optimums, *A. perplexa* fireflies find this locality suitable to dwell, while *S. substriata* fireflies are found in very small numbers.

The Fourier spectra of three species of fireflies — two Japanese species *Luciolacruciata* and *Luciolalateralis*, and one Indian species *A. perplexa*— were analysed in control and under a strong static magnetic field [Goswami et al., 2025]. It was found that the number of harmonic contents on the Fourier transform plots decreased under the high magnetic field. This pointed points towards a certain type of filtering of the pulses, which could be compared with a typical band stop filter called

notch filter. A comparison was made with a Fourier spectrum of the flashes from the species *A.perplexa* at a low temperature, and the phenomenon was found to be similar.

In a very recent study, when *A.perplexa*fireflies were placed in static electric fields their flashes were observed to lengthen suddenly [Borah and Gohain Barua, 2026], as shown in Figure 3. In the absence of the field, average pulse-widths were 121 ms for the male and 195 ms for the female at 27 °C; application of the field increased those to 174 ms for the male and 296 ms for the female. Along with the lengthening, fluctuation in the duration of the pulses also increased greatly: the standard deviation became almost three times for the male, and roughly two times for the female compared to that in control. The 'threshold' values for manifestation of this effect were approximately 30–40 V/cm in the case of the males, and approximately 25–30 V/cm for the females. It was also observed that after this happening, the flash duration remained the same even after increasing the field strength to 180 V/cm. As insects were electrified in an electric field by deprivation of their negative charge [Kakutani et al., 2012], therefore it was inferred that the "charging" of a firefly completed immediately after the process got started. The flashes emitted in presence of the static electric field bore a striking resemblance to the ones emitted in the low temperature [Borah et al., 2023], and so it was hypothesized that the electrification of the firefly made it "feel" a bit colder. That is, in the field, the firefly experienced a stress similar to the one experienced in the low temperature. In the study at low temperature [Borah et al., 2023], the average pulse-width was measured as 215 ms for the male and 307 ms for the female of this species at 20°C. In the exponential fittings of the values of pulse-width obtained at different temperatures in that study, the values of 174 and 296 ms in the DC electric field were noticed to be the ones obtained at approximately 22°C in the case of males and 20°C for females, respectively. Hence the speculation that the DC electric field made the male and female fireflies "feel like" 22 °C and 20°C, respectively, in the prevailing room temperature of 27°C. In future, experiments should be conducted to find out whether all the insects experience similar cooling type of stress under a DC electric field. In the AC electric field, the problem of ejection of electrons from the cuticle layer did not arise as the voltage alternated periodically; hence no change in the pulse width.

An investigation was carried out for finding the relationship between inter-pulse interval and temperature on males of the Japanese species *Luciolacruciata* at five different sites in central Japan.

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The study established that inter-pulse intervals linearly decrease as the ambient air temperature increases [Iguchi, 2010]. In all probability, high temperature increases the neural activity that stimulates the release of the primary neurotransmitter octopamine, which triggers the firefly lantern.

It will be interesting to observe the firefly pulses in a high-frequency electromagnetic field. Exposing four different types of insects in electromagnetic fields of frequencies from 2 GHz to 120 GHz, it was found that the microwave power was absorbed and the absorbed power generally increased at and above 6 GHz — with the suggestion that this absorption might cause dielectric heating [Thielens et al., 2018]. However, for that hypothesis to be true, the firefly-flashes will have to become shorter in an electromagnetic field.

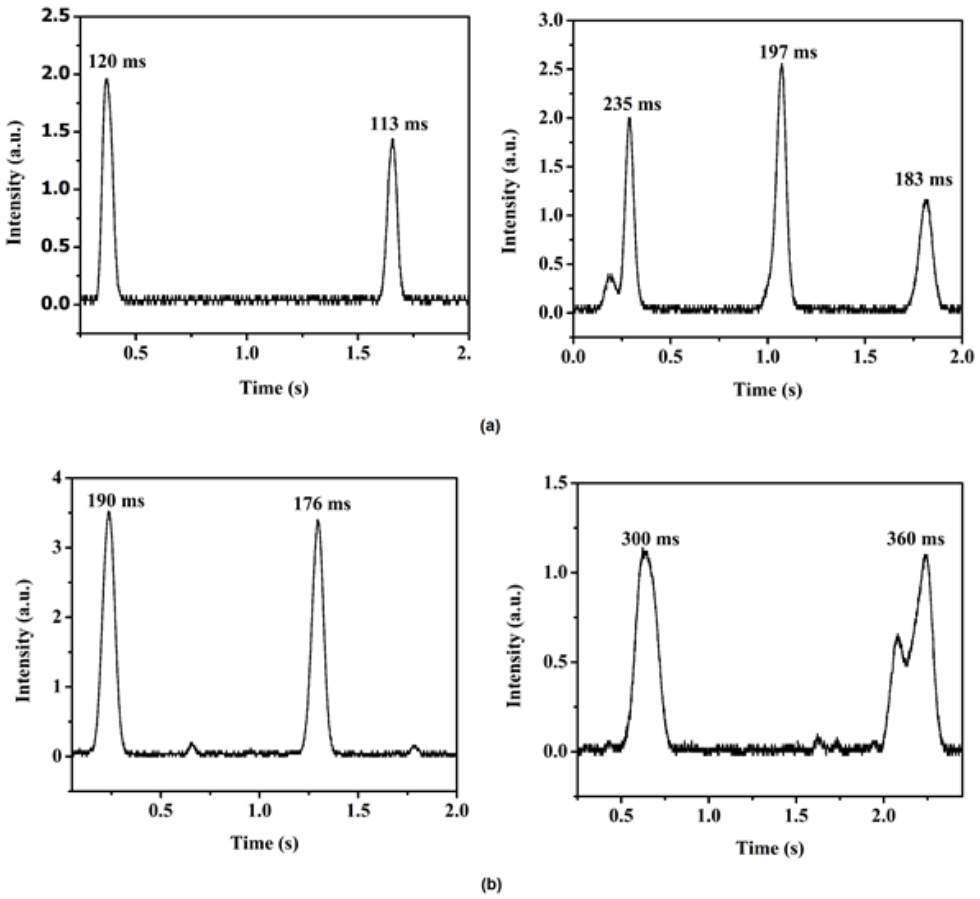


Figure 3. Flashes of the firefly *A. perplexa* at normal and under a static electric field [Borah and Gohain Barua, 2026]. **(a)** Male firefly flashes (left) lengthens immediately on application of the electric field (right). **(b)** Female firefly flashes (left) similarly broaden under the electric field (right).

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