# Effects of temperature and light availability on juvenile bull kelp sporophytes *Nereocystis luetkeana*: Informing better restoration practices on understory bull kelp

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**ABSTRACT**

Kelp forests are globally important ecosystems that provide critical ecological services, including coastal protection, habitat engineering, carbon sequestration, and nutrient cycling. In this study, I examined the effects of two abiotic factors, temperature and light, on the growth and photosynthetic efficiency of juvenile bull kelps *Nereocystis luetkeana*. Samples were placed in four treatments under ambient temperatures of 11 °C and elevated temperatures of 15 °C (± 2.5 °C), and two different ambient light intensities (average 2 μmol photons $m^{-2}$ $s^{-1}$ and 40 μmol photons $m^{-2}$ $s^{-1}$) for 7 days. These two physiological parameters operated on two distinct time frames and revealed different effects of temperature and light on the bull kelps. Chlorophyll fluorescence, the measurement of photosynthetic efficiency, declined after the acclimation period and was able to recover without significant differences between all treatments. Within the growth metric, overall growth rate and stipe elongation rate were governed by temperature and light in varying degrees. Temperature had a larger effect on the overall growth rate, whereas light had a bigger effect on the stipe elongation rate. This experiment showed the intricate nature of kelp tissues, allocating energy toward different tissue types under two separate abiotic drivers.

## INTRODUCTION

Kelp forests (Order Laminariales) are key habitat forming species along the coastal regions of temperate and subpolar seas globally (Krumhansl et al. 2016). They are incredible ecosystem engineers which support major community diversity and productivity in coastal habitats (Brady-Campbell et al. 1984, Mann 1973, Reed et al. 2008, Teagle et al. 2017). They provide three-dimensional habitat structures that give homes to numerous commercially and ecologically important species (Steneck et al. 2002, Smale et al. 2013). Along with that, kelp forests also offer coastal protection through wave attenuation, which shield the sediment against erosion and flooding (Morris et al. 2020). More significantly, kelp forests have shown amazing ability to sequester carbon dioxide. Strongly autotrophic seaweed communities worldwide can take up 1.5 Pg C year−1 through their net-production (Krause-Jensen & Duarte 2016). However, they are also among the most vulnerable marine ecosystems to climate change (Ruane 2024). Over the past century, 40-60% of kelp forests worldwide have been lost or degraded (United Nations Environment Programme 2023). Now more than ever, kelp conservation is central to climate change mitigation strategies (Eger et al. 2025).

In order to protect our irreplaceable kelp forests, we need to understand what is afflicting them. Kelp forests are threatened by numerous anthropogenic and climatic factors including sedimentation (Merrill & Gillingham 1991a, Cheney et al. 1994, Shaffer & Parks 1994, Wernberg et al. 2005), industrial chemicals (Antrim et al. 1995, Hopkins & Kain 1978, Chung & Brinkhuis 1986), water motion (Kitching et al. 1941, Eckman et al. 1989), UV radiation (Swanson & Druehl 2000, Hoffman et al. 2003), temperature (Davison & Davison 1987), and light availability (Flukes et al. 2014, Layton et al. 2019, Stuart et al. 2025).

In this study, I aim to examine two crucial factors: temperature and light. Temperature has been increasingly essential in ecological studies due to it being one of the major climate change drivers (Wernberg et al. 2024). In previous studies, higher temperatures reduced enzymatic activities and photosynthesis rate in Saccharina latissima (Davison & Davison 1987). This can lead

to kelps having to use more energy to grow under the rising temperature. Moreover, warming waters can bring many prevalent invasive species into local ecosystems (Norton 1977, Kain 1969, Thom & Hallum 1990, Britton-Simmons 2004), which in turn escalates the competition.

As for light, kelp forest canopy density and patch size can strongly influence understory assembly. Juvenile canopy forming kelp sporophytes are part of the understory community, and can be heavily impacted by light availability (Flukes et al. 2014, Layton et al. 2019, Stuart et al. 2025). Dense canopy-forming kelps can shade their juvenile sporophytes from the light, which can alter the dynamics of the kelp forests.

Major canopy-forming kelp species worldwide are *Macrocystis pyrifera*, *Nereocytis luetkeana, Ecklonia radiata, Eualaria fistulosa, Laminaria hyperborea*, and *Lessonia* spp. (Hollarsmith et al. 2024, Stuart et al. 2025). *N. luetkeana* is the dominant, canopy-forming species in inner basins of the Salish Sea, a large inland sea spanning Washington State and British Columbia, where this study took place (Kruckeberg 1991). It provides forest structure to key local species including salmonids *Oncorhynchus* spp., rockfish *Sebastes* spp., and dungeness crab *Cancer magister* (Duggins 1988, Shaffer & Parks 1994, Shaffer 2004). The primary objective of this study is to quantify the thermoacclimation and photoacclimation of macroscopic growth and photosynthetic efficiency of a single population of *N. luetkeana* under ambient temperatures of 11 °C and elevated temperatures of 15 °C (± 2.5 °C), and two different ambient light intensities (average 2 μmol photons $m^{-2}$ $s^{-1}$ and 40 μmol photons $m^{-2}$ $s^{-1}$) to better inform current restoration practices under rising global temperatures.

## MATERIALS & METHODS

### Plant Material Preparation

Juvenile *N. luetkeana* sporophytes were collected from Friday Harbor Laboratories, Washington, USA. A total of 24 samples were collected, consisting of 7 collected near FHL Dock subtidally on May 13th, 2026 and 17 collected from FHL Dock on May 14th, 2026 (Friday Harbor Laboratories, San Juan Island, WA, USA, 48.54517° N, -123.01267° W). The length between the holdfast and the end of the pneumatocyst was under 25 cm for all samples collected. The samples were threaded into plastic ropes and zip tied securely. The two ends of the ropes were tied around heavy objects, so the ropes and the holdfast were close to the bottom of the tanks. There were a total of 4 ropes, and each rope had 6 *N. luetkeana* 15 cm apart from each other. Each tank is 23 cm in height and 200,330 $cm^{3,}$ in volume, which equals 200.33 liters of water. The acrylic tanks were located outdoors, south facing, and used natural unfiltered sea water (NSW); source point was 5 m depth from San Juan Channel at the mouth of the harbor. Two tanks that were later heated were located closer to the building to facilitate power usage (Fig. 1).

### Acclimation Period

There were 7 days of acclimation period and then 7 days of experimental period. Since there were two testing variables: light intensity and temperature, I acclimatized the samples to shaded conditions for 7 days, then added the temperature variable when I started the experiment. Two tanks were set up for acclimation, and each tank had two ropes with samples in the and different layers of shade cloth over them. During the acclimation period, the Eelgrass Lab shade cloths were used. One tank was set up to high light intensity, and the other was set up to low light intensity. Since it was filtered ambient light, the light intensity varied throughout and between the days. Both tanks were maintained at ambient temperature unheated for the acclimation period. Light intensity and temperature measurements were recorded using LI-COR LI-250A Light Meter (LI-COR, Inc., Lincoln, NE, USA) and TP300 digital thermometer. During the acclimation period, the highest light intensity for the high light tank was 250 μmol photons $m^{-2}$ $s^{-1}$ and 115

μmol photons $m^{-2}$ $s^{-1}$ for the low light tank when the direct light intensity was 1,050 μmol photons $m^{-2}$ $s^{-1}$. During the same acclimation period, the ambient temperature was between 8.5 °C to 12.5 °C for the low light tank; the ambient temperature was between 8.5 °C to 16.5 °C for the high light tank.

**Experimental Treatments**

After 7 days of acclimation period, 4 ropes of samples were transferred to their own unique treatment tank. There were a total of four treatments: low temperature low light, low temperature high light, high temperature low light, and high temperature high light. For this portion of the experiment, ACE sun-filtering black shade cloths (Product #8397937) were used for all the experimental treatments to modify the light conditions. Highest direct light intensity during the experiment was 1764.3 μmol photons $m^{-2}$ $s^{-1}$. Under the same conditions, high light intensity tanks had 45.77 μmol photons $m^{-2}$ $s^{-1}$ and low light intensity tanks had 2.59 μmol photons $m^{-2}$ $s^{-1}$. As for the temperatures, the low light tank had average ambient temperature 10.5 °C (8.5 °C ~ 12.5 °C) and the high light tank had average temperature 11.5 °C (9.5 °C ~ 13.5 °C). Thus, the heated tanks were set to 4 °C higher than the ambient temperature. INKBIRD ITC-306T Plug and Play Temperature Controllers (INKBIRD, n.d.) and HL-299T Titanium Tube Aquarium Heaters were used to control the temperatures. For the heated tanks, the temperatures were controlled at 14.5 °C (12.5 °C ~ 16.5°C) for the low light tank, and 15.5 °C (13.5 °C ~17.5 °C) for the high light tank. Since the experiment was done using outdoor tanks, the weather conditions were uncontrolled and variable during the experimental period, including rain and high winds on some days.

**Chlorophyll fluorescence**

Chlorophyll fluorescence ($F_v/F_m$) was measured using Hansatech Instruments Pocket PEA Chlorophyll Fluorimeter at 3,500 watts for the samples before the acclimation period as a control. Measurements were taken 5 cm above the pneumatocyst on the blade. Chlorophyll fluorescence

was also measured after the acclimation period, and after the entire experiment. Samples were selected at random, and each condition had at least 3 replicates. Chlorophyll fluorescence was the measurement of photosynthetic efficiency for plant biology research.

**Physical Growth Rate**

Hole punch method was used to measure the physical growth rate of the *N. luetkeana* (Parke 1948). It was implemented after the acclimation period and before the start of the experiment. I first measured the length of holdfast to the end of pneumatocyst, pneumatocyst itself, and blade itself. I then punched holes with a 1 cm diameter cork borer, following 5 cm intervals above the pneumatocyst on the blade, and labelled them in alphabetical order (Fig. 2). After punching the holes, I recorded the length from the end of the pneumatocyst to the first hole, and lengths between subsequent hole punches. I took measurements every 2 days of 2 samples per treatment. The growth rate (increase in cm/day) and stipe elongation rate (cm/day) was quantified by subtracting the previous measurement from the following measurement.

**Statistical Analysis**

Given that the experiment had a small sample size, I used the non-parametric Kruskal-Wallis test for analyzing physical growth rate and chlorophyll fluorescence. I plotted the average growth rate of the four treatments and found the trendlines for each of them. I then compared the coefficients of the trendlines of the treatments.

## RESULTS

Through the Kruskal-Wallis test, the p-value of the growth rate between the four treatments was 0.3761 ($p > 0.05$). This showed that the data was not statistically significant. As for the chlorophyll fluorescence, the p-value was 0.07425 ($p > 0.05$) for the four treatments at the end of the experiment, which is also not statistically significant. However, the p-value of the chlorophyll fluorescence was lower than the growth rate. The chlorophyll fluorescence decreased after the acclimation period, and recovered at the end of the experiment. The high light intensity treatment had a lower chlorophyll fluorescence measurement than the low light intensity treatment during the acclimation period. At the end of the experiment, lower temperature treatments showed higher chlorophyll fluorescence measurements than higher temperature treatments (Fig. 3).

The trendlines for average growth rates of the four treatments showed two different trajectories. The coefficients of low temperature trendlines are all positive: 0.225 for low light intensity and 0.1 for high light intensity. Whereas, the coefficients of high temperature treatments are all negative: -0.5625 for low light intensity and -0.75 for the high light intensity. This means that low temperature treatments had an increase in average growth rate, and high temperature treatments had a decrease in average growth rate. As for the light conditions, higher light intensity treatments both led to a lower growth rate under the same temperature conditions (Fig. 4).

I also performed the Kruskal-Wallis test on the average stipe elongation rate for the four treatments ($p= 0.1726$, $p > 0.05$). Even though it was not statistically significant, the low light intensity treatments both had larger increases in average stipe length than the high light intensity treatments. Low temperature low light treatment had the highest stipe elongation rate (Fig. 5).

## DISCUSSION

In this study, I examined two physiological traits of juvenile *N. luetkeana* to study the comprehensive effects of temperature and light availability. These two physiological parameters operate on very different time frames.

For chlorophyll fluorescence, I was able to capture the full photoacclimatization of the samples, and as for physical growth, I had just begun to see the trends in 7 days. For both parameters, I observed that juvenile sporophytes performed better under lower light conditions. This finding was similar to previous studies because *N. luetkeana* have adapted to this benthic life stage and tolerated extreme light limited lifestyles. Studies have shown that kelp species can live under other canopy-forming algae that reduce bottom light availability by 60% (Machalek et al. 1996, Clark et al. 2004, Schiel & Foster 2015). It has also been shown that many understory kelp species are good at capturing lightflecks for photosynthesis (Wing & Patterson 1993). My experiment used shade cloth to filter ambient light, which happened to create a similar effect. Experiments done in laboratory settings also proved that *N. luetkeana* juvenile sporophyte growth peaked between 15 μmol photons $m^{-2}$ $s^{-1}$ and 30 μmol photons $m^{-2}$ $s^{-1}$ (Vadas 1972). The higher light intensity in my experiment averaged around 40 μmol photons $m^{-2}$ $s^{-1}$, which could photoinhibit the growth of the juvenile sporophytes and cause them to have a lower growth rate.

On the other hand, limited light availability also pushed the *N. luetkeana* to have a higher stipe elongation rate. Hurd (1916) first proposed that the stipe elongation was promoted by weak light intensity in deep water, and inhibited by high light intensity at the surface of water; this prioritizes stipe elongation to get juveniles sporophytes to the water surface and then slows growth once they reach the surface. However, later studies showed that the depth of water was not the major factor that governed the stipe elongation (Nicholson 1970, Foreman 1970). Duncan (1973) found that the spectral irradiation had the greatest effect on stipe elongation among other environmental parameters, such as salinity, temperature, and nutrients. Further studies showed that the elongation could be triggered by the ratio of red to far red light, which is a response

mediated by phytochrome (Duncan 1971, Duncan & Foreman 1980). The ratio of red to far red light is usually altered by shading. The shade cloth used to filter ambient light in my experiment perfectly mimicked the shaded conditions that *N. luetkeana* would experience in real life; with the higher shaded conditions mimicking conditions on the benthos and the less-shaded conditions mimicking surface or near-surface conditions; therefore sporophytes in the higher shaded conditions were allocating more energy towards stipe elongation. My findings also supported the prior research that *N. luetkeana* experiencing higher shades had a greater stipe elongation rate. This work is an example of the complex way that kelp tissues respond to environmental stimuli and reallocate energy to different tissue types.

Previous research had indicated that *N. luetkeana* sporophytes can survive at a range of -1.5 °C to 18 °C (Lüning & Freshwater 1988), with an optimal temperature range between 10 °C to 15 °C in laboratory settings (Vadas 1972). My findings revealed the nuances in that temperature range. The lack of change in photosynthetic efficiency (Fv/Fm) showed that the sporophytes were not truly stressed, but the growth was still being affected. With ambient temperatures just 4 °C apart, the juvenile *N. luetkeana* can have drastically different trends of growth. Treatments with ambient temperature 11 °C (± 2.5 °C) all had positive growth rate trends; on the contrary, treatments under elevated temperatures of 15 °C (± 2.5 °C) all had negative growth rates. Therefore, the decline in chlorophyll fluorescence after the acclimation period across all treatments was likely caused by a combination of higher temperature (+1 °C) compared to in-situ conditions (NVS Data Explorer 2026) and photoinhibition by the light shone through the front of the acrylic tanks .

The experiment was conducted under mesocosm conditions with ambient light, temperature, and natural sea water from the original habitat. To further control the natural environmental fluctuation and isolate the target variables, future research can be conducted under controlled light intensity and weather conditions using filtered natural sea water. On Day 3 of the experiment, the weather was rainy and windy. Thus, it might lead to the drop in growth for the samples. I used unfiltered seawater, so during the experiment, the ropes and the tanks were heavily fouled by diatoms, which could lead to minor barriers for the samples to capture light; using

filtered seawater could prevent excessive fouling (Fig. 6). The tank positions would ideally be randomized without equipment constraints. Experiments can also be designed to test more variables. Further studies can investigate the dynamics of various understory algae species under similar conditions.

Although the results were not statistically significant due to the small sample size, my experiment was still informative because there were no previous studies on temperature and light availability effects on juvenile bull kelp *N. luetkeana*. In addition, I recorded two different physiological parameters, growth and chlorophyll fluorescence, of *N. luetkeana.* This gave us a holistic view on bull kelps' responses to the two drivers. Within the growth measurements, we can also observe distinct trends when focusing on different components. For the overall growth rate of *N. luetkeana*, temperature is the larger factor. Lower temperature allowed the samples to have a positive growth rate trend, and higher temperature led the samples to have a negative growth rate trend. However, when we look at stipe elongation rate, light is the bigger factor. Stipe elongation rate of the low light intensity treatments was at least 3 times greater than the high light intensity treatments. This is an example of the intricate way that kelp tissues can respond to environmental stimuli and reallocate energy to different tissue types. When considering restoration practices, temperature is a more crucial factor than light in general. If permitted, prioritizing sites with stable sea water temperatures can benefit the *N. luetkeana* population more than managing shading conditions. As for aquaculture farming, *N. luetkeana* juvenile sporophytes need less light at this stage of their lives; people raising juvenile sporophytes in land-based tanks should add shade cloths for greater production. Maintaining kelp forest ecosystems is crucial for our on-going battle against climate change.

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**FIGURES**



**Figure 1.** Experimental setup. Four south-facing, acrylic glass tanks located outdoors. Two heated tanks located closer to the building. All tanks covered in shade cloth.



**Figure 2.** Example of hole punch method on *Nereocystis luetkeana* sample.

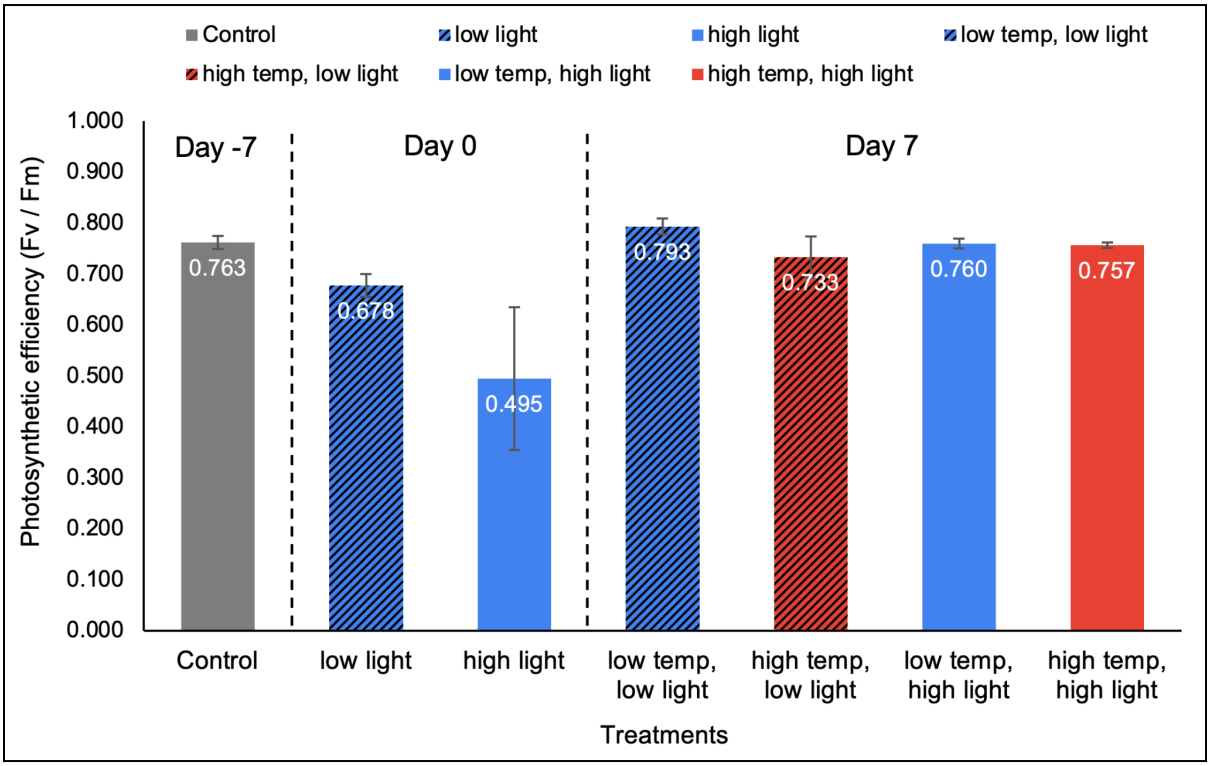



**Figure 3.** Average chlorophyll fluorescence of *Nereocystis luetkeana* at the start of the experiment compared to the end of the experiment. Control was measured on the day of collection. Error bars represent the standard deviation. n=3 per bar.

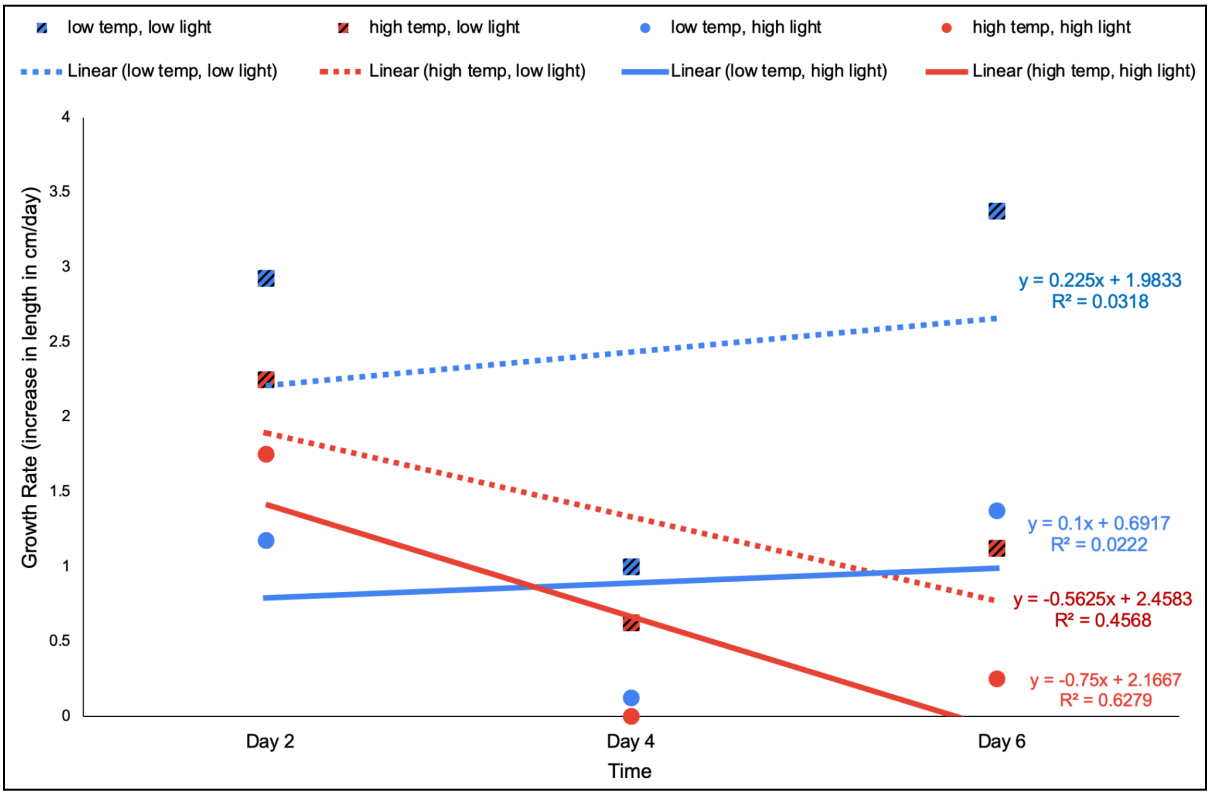



**Figure 4.** Average growth rate of *Nereocystis luetkeana* under four different treatments over the experimental period. Trendlines show the growth trajectories of each treatment.

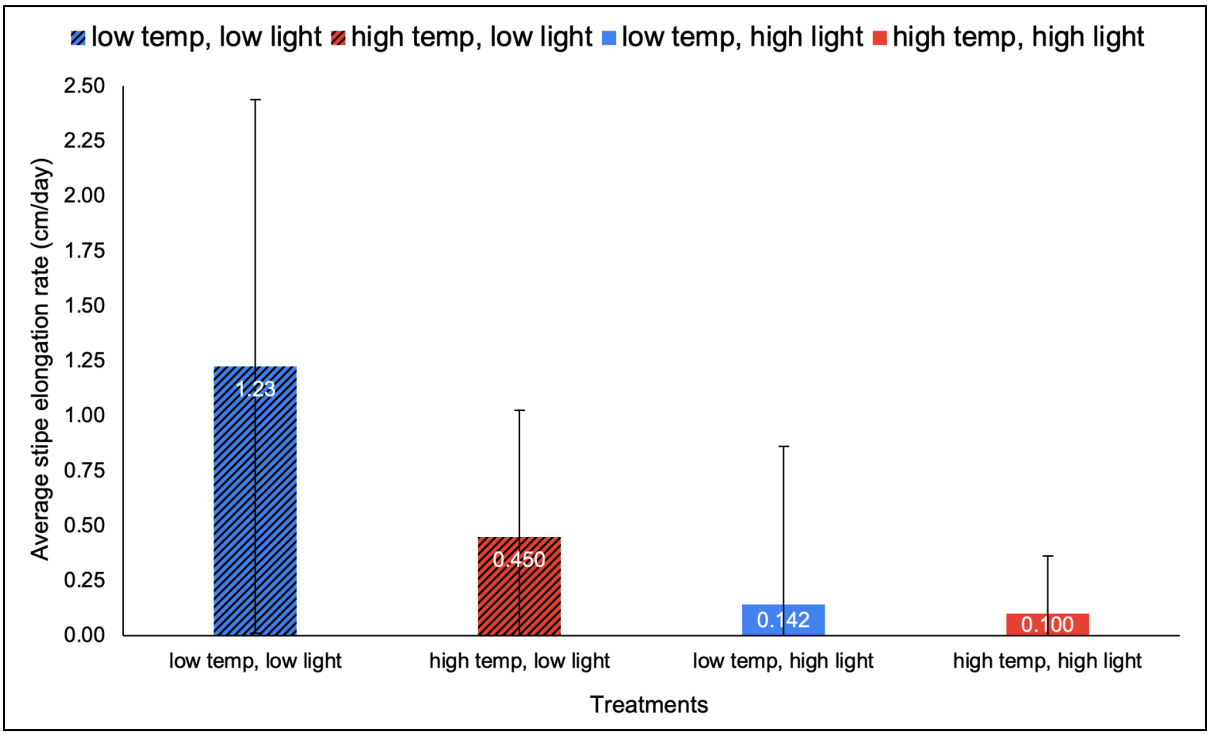



**Figure 5.** Average stipe elongation rate of the four treatments for the entire experiment (7 days). Error bars represent standard deviation.



**Figure 6.** Tanks covered with diatoms at the end of the experiment.

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