

Plants can acclimate and grow healthily under a range of temperatures, and here photosynthetic performance generally correlates with overall plant performance (Lambers & Oliveira 2019c, Yamori et al 2014, Figure 1). The range of temperatures plants can safely acclimate to depends on their evolutionary and breeding history. The optimal growth temperatures for a given species or cultivar will generally reflect their photosynthetic type and climate of origin; warmer temperatures closer to the equator and cooler temperatures for plants that evolved at higher latitudes, varying with microclimates within latitudinal generalizations (Berry & Bjorkman 1980). The standard temperature control range (5 to 35°C) in growth chambers and rooms can provide the optimal growth temperatures for virtually any plant. Growth temperature affects the vapor pressure deficit and interacts with light intensity (PPFD), light quality, nutrition, and CO2 concentration to set the course of growth for your plants. In this way, definitively optimal growth temperatures can be challenging to predict for a given growth chamber situation. Deviation from optimal growth temperatures (both warmer and cooler) tends to cause plants to invest more in roots and decreases their shoot to root biomass ratio (shoot:root) (Lambers & Oliveira 2019a).

Warmer temperatures toward optimal growth temperatures will speed up growth and development. From seed germination and emergence through to flowering and seed maturation, to a threshold, warmer temperatures generally shorten lifecycles. Because of the strong correlation between accumulated thermal time and plant development, growing degree days are a widely used index in agriculture to help determine when to plant crops and how long before harvest (Lambers & Oliveira 2019a). Daytime temperatures, when plants are actively photosynthesizing, generally have more control over growth rate than nighttime temperatures. In lettuce (*Lactuca sativa* L.), tomato (*Solanum lycopersicum* L.), and soybean (*Glycine max* L.), nighttime temperatures 7°C lower or higher than constant growth at 25°C did not significantly affect

biomass gain at the end of the experiment (Frantz et al 2004). Similarly in Arabidopsis, growth at 24/16°C day/night was not significantly different than growth at constant 24°C (Pyl et al 2012). In contrast to dicots, where their circadian system has more control over growth, leaf extension in grasses (monocots) is more responsive to a day/night temperature differential (Matos et al 2014, Poiré et al 2010). In some species, often woody, low nighttime temperatures can inhibit overall growth. In other species, elevated nighttime temperatures can impair reproductive investment (Jing et al 2016). Nighttime temperatures that are 5°C less than daytime temperatures, or a constant day/night temperature, are commonly used in growth chambers (Langhans & Tibbitts 1997). Outside, nighttime temperatures routinely drop >5°C from daytime in many growing regions. If your goal is to mimic plant growth closer to the field, setting nighttime temperatures lower than daytime helps to entrain the circadian system and metabolic cycling closer to plants grown outside (Kronenberg et al 2020, Matsubara 2018, Poorter et al 2016).

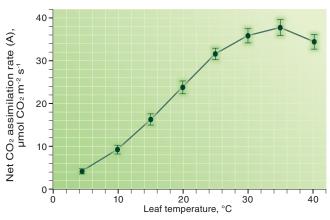


FIGURE 1: Response of photosynthetic rate (net CO_2 assimilation rate, A) to leaf temperature (°C) of the C_4 perennial grass Miscanthus x giganteus. Measurements of A were taken at 1800 PPFD and 400ppm ambient cuvette CO_2 concentration. Plants were grown in BioChambers GC-20 (TPC-19) growth chambers at 27/20°C day/night temperatures, 14 hour photoperiod, and under a growth PPFD of 550 (\pm 50) at the top of the leaves. Symbols are the mean average \pm standard error, n = 6 different plants/leaves. Straight lines connect each symbol.

The difference between day and night growth temperatures (DIF = day - night) can markedly affect stem elongation and plant height in maize (Zea mays L.), tomatoes (S. lycopersicum L.), cucumbers (Cucumis sativus L.), and lilies (Lilium sp.), among others (Erwin & Heins 1995). A natural positive DIF (day warmer than night) causes plant height to more closely match that of plants growing outside. To a point, the greater the positive DIF, the greater the stem elongation and plant height in DIF sensitive species. Moving towards neutral and into negative DIF, plants become shorter (Erwin & Heins 1995). The mechanisms underlying the DIF plant height response involve the plant hormone gibberellin and phytochrome B photoreceptor (Patil & Moe 2009, Stavang et al 2005). Including and adding far-red and/or lowering the R:FR in your light source enhances the stem elongation effects of positive DIF (Friesen 2020, Patil & Moe 2009). Temperature directly affects phytochrome B; warmer temperatures result in some of the same effects as increasing the amount of far-red and lowering the R:FR (Legris et al 2016, Legris et al 2017, Hayes et al 2021, Klose et al 2020). Retrospectively, understanding how temperature directly affects phytochrome B sheds clarity on earlier experiments, explaining why day extension incandescent lighting (low R:FR, appreciable far-red) counteracted the plant shortening effects of a negative DIF in Campanula (Moe et al 1991).

Beyond temperatures a plant can acclimate to, high or low temperatures can become stressful, markedly inhibiting growth (possibly towards mortality), often with visible symptoms on the plant body. Exposure to stressful temperatures may be intentional, in the case of temperature stress experiments. Occasionally temperature stress can be unintentional; transfer of plants grown at high to low, or low to high temperatures can be stressful during the transition, even if the plant can eventually acclimate to the new growth temperatures. Low temperature stress can be caused by chilling (low >0°C temperatures) or sub-zero (<0°C) temperatures, and tolerance of either can be independent of each other (Ruelland et al 2009). Acclimation and tolerance of chilling temperatures and higher PPFD involve many of the same processes while at the same time exacerbating the potentially stressful effects of either one (Lambers & Oliveira 2019c, Lambers & Oliveira 2019d). Visible signs of chilling stress can include photobleaching (chlorosis) or red/purple/blue pigmentation (anthocyanins) (Lambers & Oliveira 2019c, Saltveit & Morris 1990, Taylor et al 1975). High temperature stress can also cause visible photobleaching (chlorosis) and leaf scorching, but often disproportionally impairs reproductive development (pollination and seed development) (Sage et al 2015, Wahid et al 2007). Stressful growth temperatures are species specific and can be <15°C for maize (Zea mays L.) and >25°C for some CANOLA (Brassica sp.)

cultivars (Long & Spence 2013, Morrison et al 1989).

Finally, you can make use of growth chamber temperature control to aid in seed germination and timely flowering towards your plant growth goals. Growth chambers and rooms can be used like a giant fridge to stratify large numbers of seeds. After planting, some seeds require diurnal temperature changes to successfully germinate, which growth chambers can also provide. Onions (*Allium cepa L.*), winter cereals, and some ecotypes of Arabidopsis require vernalization for timely flowering, and growth chambers can provide these conditions as well (Lambers & Oliveira 2019b). Lastly, gradual user controlled temperature changes can help transition to flowering in photoperiodically sensitive plants; with a springtime warming trend for long-day plants and autumnal cooling trend for short-day plants (Lambers & Oliveira 2019b).

Plant tissue temperature can differ from growth chamber setpoint temperature, especially in equipment with fluorescent/ halogen or HID (metal halide + high pressure sodium) lighting. Radiant heat from these older light sources can raise leaf temperature several °C above chamber set-point, depending largely on plant distance from the lights. LED lighting systems generally emit less radiant heat compared to older lighting systems; however, there are often still some measurable radiant heat effects (Nelson & Bugbee 2015). Occasionally, plant tissues can be lower than air temperature set-point through evaporative cooling from transpiration (Hicklenton & Heins 1997). Air movement within a growth chamber also affects plant tissue temperatures; more air movement causes plant tissues to be closer to chamber set-point whereas heat can build up in areas with little air movement. Accurate independent reporting of plant tissue temperature is especially important for temperature related experiments. Thermocouples in contact with the underside of leaves (and other tissues) or infrared thermometers pointed downwards on leaves in close range are two methods to accurately measure tissue temperature (Ehleringer 2000, Hicklenton & Heins 1997).

References

Berry J, Bjorkman O. 1980. Photosynthetic Response and Adaptation to Temperature in Higher Plants. Annual Review of Plant Physiology, 31: 491-543.

Ehleringer JR. 2000. Temperature and energy budgets. In: Plant Physiological Ecology: Field methods and instrumentation, pp. 117-135: Springer.

Erwin JE, Heins RD. 1995. Thermomorphogenic Responses in Stem and Leaf Development. HortScience, 30: 940-949.

Frantz JM, Cometti NN, Bugbee B. 2004. Night Temperature has a Minimal Effect on Respiration and Growth in Rapidly Growing Plants. Annals of Botany, 94: 155-166.

Friesen P. 2020. How far-red photons affect plant growth and development: a guide to optimize the amount and proportion of far-red under sole-source electric lights. BioChambers Inc., 1-8. https://www.biochambers.com/pdfs/farRed.pdf Hayes S, Schachtschabel J, Mishkind M, Munnik T, Arisz SA. 2021. Hot topic: Thermosensing in plants. Plant, Cell & Environment, 44: 2018-2033.

Hicklenton PR, Heins RD. 1997. Temperature. In: Plant Growth Chamber Handbook, eds. RW Langhans, TW Tibbitts, pp. 31-42: Iowa State University, NCR-101 Publication No. 340. https://www.controlledenvironments.org/wp-content/uploads/sites/6/2017/06/Ch02.pdf

Jing P, Wang D, Zhu C, Chen J. 2016. Plant Physiological, Morphological and Yield-Related Responses to Night Temperature Changes across Different Species and Plant Functional Types. Frontiers in Plant Science, 7: 1-19. Klose C, Nagy F, Schäfer E. 2020. Thermal Reversion of Plant Phytochromes. *Molecular Plant*, 13: 386-397.

Kronenberg L, Yates S, Ghiasi S, Roth L, Friedli M, et al. 2020. Rethinking temperature effects on leaf growth, gene expression and metabolism: Diel variation matters. Plant, Cell & Environment, 1-15. https://onlinelibrary.wiley.com/doi/full/10.1111/pce.13958

Lambers H, Oliveira RS. 2019a. Growth and Allocation. In: Plant Physiological Ecology, pp. 385-449: Springer.

Lambers H, Oliveira RS. 2019b. Life Cycles: Environmental Influences and Adaptations. In: Plant Physiological Ecology, pp. 450-486: Springer.

Lambers H, Oliveira RS. 2019c. Photosynthesis, Respiration, and Long-Distance Transport: Photosynthesis. In: Plant Physiological Ecology, pp. 11-114: Springer.

Lambers H, Oliveira RS. 2019d. Plant Energy Budgets: Effects of Radiation and Temperature. In: Plant Physiological Ecology, pp. 279-290: Springer.

Langhans RW, Tibbitts TW. 1997. Plant Information Table. In: Plant Growth Chamber Handbook, pp. 219-225: Iowa State University, NCR-101 Publication No. 340. https://www.controlledenvironments.org/wp-content/uploads/sites/6/2017/06/Plant_Info_Table-1.pdf

Legris M, Klose C, Burgie ES, Rojas Cecilia Costigliolo R, Neme M, Hiltbrunner A, Wigge PA, Schäfer E, Vierstra RD, Casal JJ. 2016. Phytochrome B integrates light and temperature signals in Arabidopsis. Science, 354: 897-900. Legris M, Nieto C, Sellaro R, Prat S, Casal JJ. 2017. Perception and signalling of light and temperature cues in plants. The Plant Journal, 90: 683-697.

 $Long SP, Spence AK. \ 2013. \ Toward \ Cool \ C_4 \ Crops. \ \textit{Annual Review of Plant Biology}, \textbf{64}: \ 701-722.$

Matos DA, Cole BJ, Whitney IP, MacKinnon KJM, Kay SA, Hazen SP. 2014. Daily Changes in Temperature, Not the Circadian Clock, Regulate Growth Rate in Brachypodium distachyon. Plos One, 9: e100072. https://doi.org/10.1371/journal.pone.0100072

Matsubara S. 2018. Growing plants in fluctuating environments: why bother? Journal of Experimental Botany, 69: 4651-4654.

Moe R, Heins RD, Erwin J. 1991. Stem elongation and flowering of the long-day plant Campanula isophylla Moretti in response to day and night temperature alternations and light quality. Scientia Horticulturae, 48: 141-151.

Morrison MJ, McVetty PBE, Shaykewich CF. 1989. The determination and verification of a baseline temperature for the growth of Westar summer rape. Canadian Journal of Plant Science, 69: 455-464.

Nelson JA, Bugbee B. 2015. Analysis of Environmental Effects on Leaf Temperature under Sunlight, High Pressure Sodium and Light Emitting Diodes. *Plos One*, **10**: e0138930. https://doi.org/10.1371/journal.pone.0138930

Patil GG, Moe R. 2009. Involvement of phytochrome B in DIF mediated growth in cucumber. Scientia Horticulturae, 122: 164-170.

Poiré R, Wiese-Klinkenberg A, Parent B, Mielewczik M, Schurr U, et al. 2010. Diel time-courses of leaf growth in monocot and dicot species: endogenous rhythms and temperature effects. Journal of Experimental Botany, 61: 1751-1759.

Poorter H, Fiorani F, Pieruschka R, Wojciechowski T, van der Putten WH, et al. 2016. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytologist, 212: 838-855

Pyl E-T, Piques M, Ivakov A, Schulze W, Ishihara H, et al. 2012. Metabolism and Growth in Arabidopsis Depend on the Daytime Temperature but Are Temperature-Compensated against Cool Nights. The Plant Cell, 24: 2443-2469. Ruelland E, Vaultier MN, Zachowski A, Hurry V. 2009. Cold Signalling and Cold Acclimation in Plants. Advances in Botanical Research, 49: 35-150.

Sage TL, Bagha S, Lundsgaard-Nielsen V, Branch HA, Sultmanis S, Sage RF. 2015. The effect of high temperature stress on male and female reproduction in plants. Field Crops Research, 182: 30-42.

Saltveit ME, Morris LL. 1990. Overview on chilling injury of horticultural crops. In: Chilling injury of horticultural crops, pp. 3-15: CRC Press.

Stavang JA, Ernsten A, Lindegård B, Lid S, Moe R, Olsen JE. 2005. Thermoperiodic regulation of shoot elongation is mediated by transcriptional regulation of GA inactivation in pea. Plant Physiology, 138: 2344–2353. Taylor AO, Halligan G, Rowley JA. 1975. Faris banding in panicoid grasses. Functional Plant Biology, 2: 247-251.













