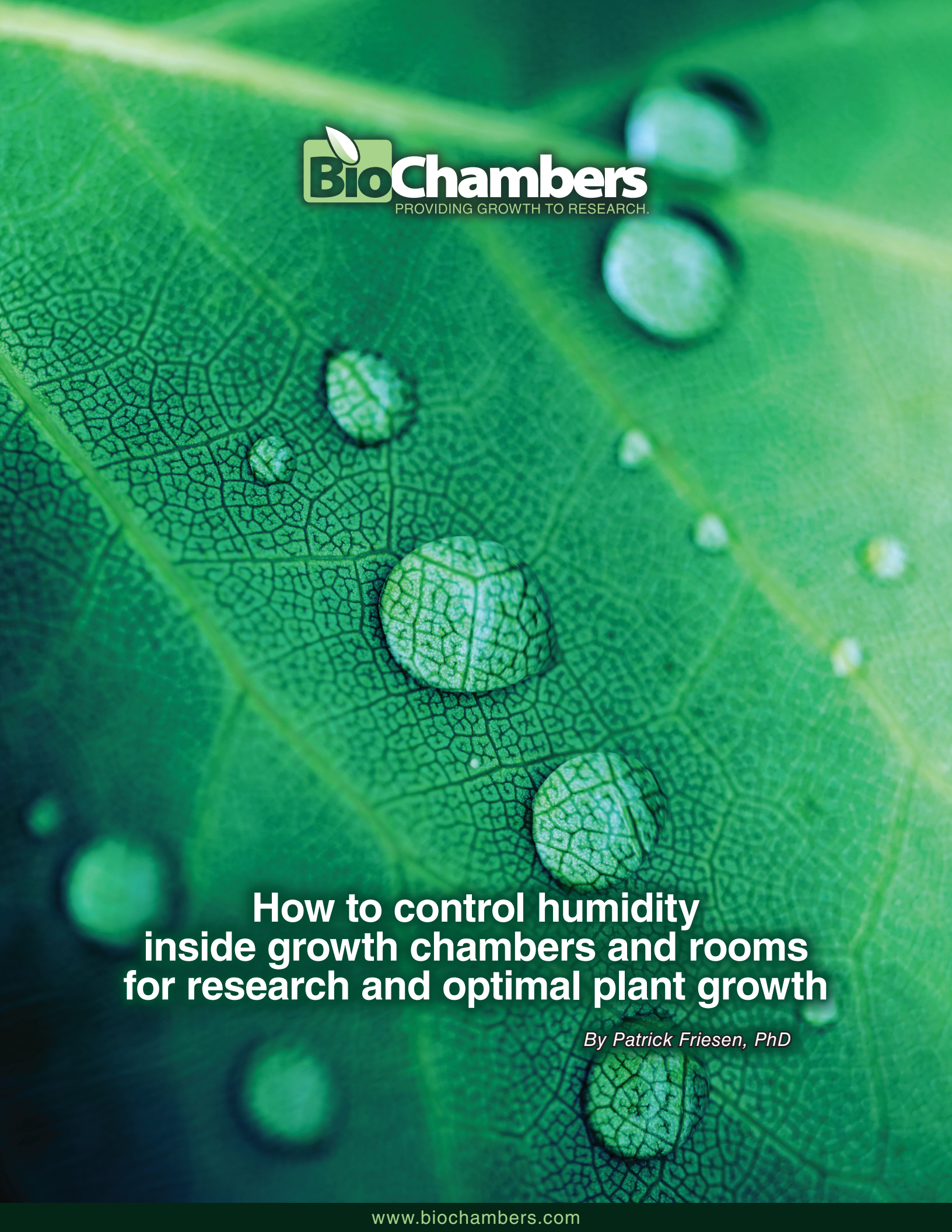

How to control humidity inside growth chambers and rooms for research and optimal plant growth

By Patrick Friesen, PhD

How to control humidity inside growth chambers and rooms for research and optimal plant growth

The humidity inside your growth chamber can affect the growth rate and health of your plants. People often use relative humidity, but the vapor pressure deficit is more robust for assessing plant growth and health. Here we review how the vapor pressure deficit affects plant growth and transpiration, how to estimate water vapor loads from plants, and other factors that can change the vapor pressure deficit inside controlled environments. Seasonal and geographic differences can change the vapor pressure deficit by over 200% in growth chambers without formal humidity control, which could affect growth by 10 to 68% in some plants.

Part 1: How the vapor pressure deficit affects plants inside growth chambers

1.1 What is the vapor pressure deficit and how does it change?

The air inside plant growth chambers or rooms "holds" more or less water vapor depending on the air temperature. Water vapor, like all gases, exerts a partial pressure, termed vapor pressure (*VP*). As air temperature increases, the *VP* required to saturate the air with water vapor also increases. The saturation vapor pressure (*SVP*) is air at 100% relative humidity (*RH*), at which point water vapor will condense, forming dew or frost on solid objects. The temperature at which a given *VP* becomes the *SVP* is called the dew point temperature (*DPT*) (Figure 1). The *VP* deficit (*vpd*) is the difference between the *VP* of air and its *SVP* at a given temperature. The *VP* deficit based on leaf temperature (*vpdL*) is the difference between the *SVP* of leaves at leaf temperature and the *VP* of the surrounding air (Figures 1 & 2). The *SVP* is used to calculate the *vpdL* as intercellular air spaces inside leaves are assumed to be saturated with water vapor. Since leaves are most often the plant organ with the greatest surface area, the *vpdL* is most useful to infer how *RH* may affect plant growth[1-4]:

$$vpd = SVP_{air} - VP_{air} \quad \text{(Equation 1)}$$

$$vpdL = SVP_{leaf\ temp} - VP_{air} \quad \text{(Equation 2)}$$

$$vpd_{air} = (^{RH\%}/_{100}) \times VP_{air\ temp} \quad \text{(Equation 3)}$$

$$RH = (VP_{air\ temp} \div SVP_{air\ temp}) \times 100\% \quad \text{(Equation 4)}$$

Lower *RH* causes a higher *vpdL*, whereas higher *RH* causes a lower *vpdL* at a given temperature. Note that any temperature difference between a leaf and the surrounding air also affects the *vpdL* (Equation 2). Leaf temperature is largely determined by the energy balance of convective heat transfer with the surrounding air, absorption of radiative heat from the light source and surroundings, and evaporative cooling from transpiration (*E*). In growth chambers and rooms, the better the control and uniformity of air temperature, and the greater the air movement around plants, the closer leaf temperature will be to the air temperature set-point through convective heat transfer. Radiative heat from electric lights inside growth chambers generally causes leaf temperatures to be 1 to 3°C higher than air temperature and this will increase the *vpdL* (Equation 2, Appendix 1).[5-7] The extent of radiative heating depends on the distance between the leaves and the lights and how much the lights radiate heat. In general, under a similar light intensity (Photosynthetic Photon Flux Density, *PPFD*), light emitting diode (LED) lighting fixtures will emit less radiant heat than high intensity discharge (high pressure sodium + metal halide) or fluorescent + halogen lighting fixtures.[5,8] Lastly, anything that causes *E* to increase (discussed in the following sections) will act to cool leaves. Occasionally leaves will drop below air temperature, especially at warmer air temperatures (>30°C) and in drier air, and this will reduce the *vpdL*.[5, 6] Accurate ways to measure leaf temperature are with a thermocouple on the underside of leaves or with an infra-red thermometer pointing downwards onto the top side of leaves.[7,9]

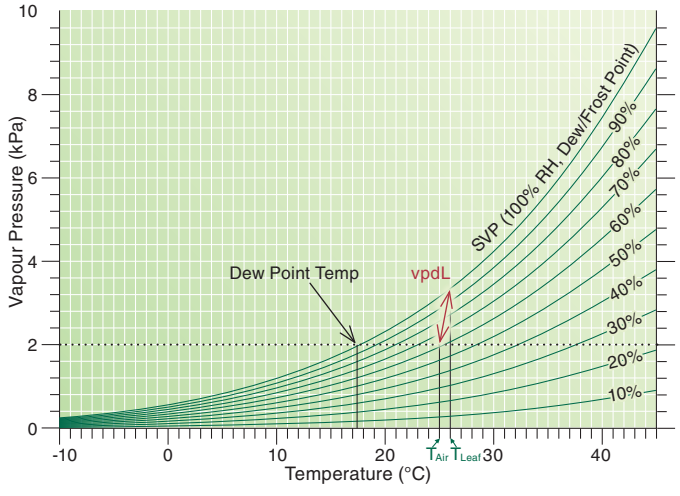

Figure 1: *SVP* curve with constant *RH* (%) lines over a range of temperatures. Here we illustrate how to estimate and interpret the *vpdL*. In this example, the growth chamber air temperature is 25°C and the leaf temperature is 26°C. The air has a *VP* of 2kPa, which means at 25°C it is at 62% *RH*, and becomes saturated (100% *RH*), at 17.5°C, its *DPT* . The *vpdL* is 3.3kPa ($SVP_{leaf\ temp}$) – 2kPa (VP_{air}) = 1.3kPa. This *SVP* curve is available as a table, allowing you to easily calculate the *vpdL* when *RH*, leaf temperature, and air temperature are known (www.biochambers.com/knowledge/SVPTable.pdf).

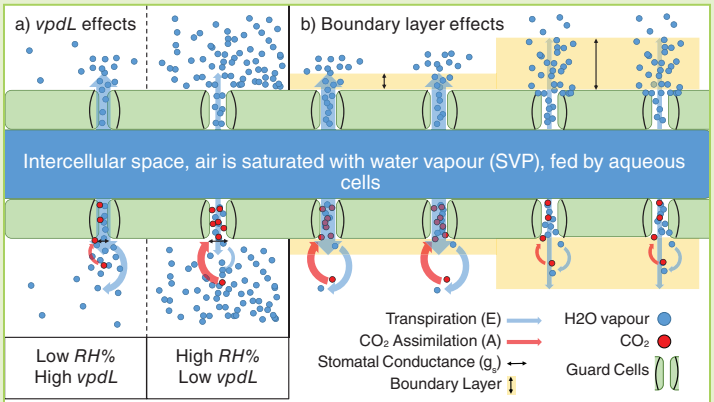

Figure 2: Illustration of how the *vpdL* and boundary layer affect *E* and *A*.

A) When the *vpdL* is high, the steep gradient in water *VP* generally causes *E* to increase. A high *vpdL* can also reduce g_s via guard cells to limit water loss, and this can reduce *A* and growth. When the *vpdL* is low, the gentle gradient in water *VP* reduces *E* and allows for greater g_s and *A*.

B) A thinner boundary layer increases g_{bl}, and acts to increase both *E* and *A*. A thicker boundary layer decreases g_{bl} and acts to reduce *E* and *A*.[2,19]

1.2 The vpdL affects plant growth and health

1.2.1 – Too high or low a vpdL can restrict plant growth

Plant leaves are covered with pores called stomata (singular stoma), surrounded by guard cells that control their size or aperture. Stomata are the site of gas exchange in plants, releasing water vapor through E while assimilating CO_2 for growth and development through photosynthesis (net CO_2 assimilation, A)[2,10,11]:

$$E = g_{wv}\,(W_{leaf} - W_{air}) \quad \text{(Equation 5)}$$

$$g_{wv} = \frac{(g_s \times g_{bl})}{(g_s + g_{bl})} \quad \text{(Equation 6)}$$

$$W_{leaf} = \frac{SVP_{leaf\ temp}}{Atmospheric\ Pressure} \quad \text{(Equation 7)}$$

$$W_{air} = \frac{VP_{air\ temp}}{Atmospheric\ Pressure} \quad \text{(Equation 8)}$$

Where W_{leaf} = amount of water vapor from leaves, and W_{air} = amount of water vapor in the air. Total conductance to water vapor (g_{wv}) is a combination of stomatal (g_s) and boundary layer conductance (g_{bl}) to water vapor, g_{bl} determined by air temperature, air movement, and the length of the leaf vector across which air is moving. Greater air movement and a shorter vector across the leaf increases g_{bl} (thinner boundary layer) whereas slower air movement and a longer vector across the leaf decreases g_{bl} (thicker boundary layer). As g_{bl} increases, E, and the rate of convective heat transfer all increase.[2] Stomatal aperture regulates stomatal conductance to water vapor (g_s), with greater stomatal aperture causing greater g_s (Figure 2). If g_s were to remain constant, water loss through E would be linearly related to increasing *vpdL*, and A would be only slightly diminished from E through lower mesophyll conductance to CO_2.[2,12] The mesophyll is the inner region of leaves beyond the stomata, and the flux of water vapor outwards reduces its ability to conduct CO_2 inwards towards the chloroplasts. Under a constant g_s scenario however, the water loss and dehydration from E would be too much for most plants to handle. Plants have evolved to find a balance in their g_s between maintaining A and mitigating water loss through E (Figure 2). As the *vpdL* increases, flowering plants sense the increase in E or decline in water status somewhere in the leaf or vasculature and close their stomata after an inherent threshold is reached, reducing g_s to conserve water.[13-15] (Figure 2). Transpirational water flux is one of several other environmental factors that regulate g_s, and in well-watered plants E will rarely be the predominant regulating signal. Other factors that regulate g_s include light intensity (*PPFD*), ambient [CO_2], whole-plant water status, and circadian/time of day effects (see Table 1).

Table 1

Inside growth chambers, g_s will change dramatically with the diurnal light cycle, increasing markedly when the lights come on, and increasing with any further increases in light intensity (PPFD).[16] During the night, when the lights are off, g_s will be quite low, and normally only a fraction of what it is during the day.[17,18] CO_2 concentrations also affect g_s, with lower CO_2 concentrations increasing g_s and higher CO_2 decreasing g_s.[16]

Stomatal opening ($\uparrow g_s$)	Stomatal closing ($\downarrow g_s$)
High temperatures	Low temperatures (stressful)
Low [CO_2]	High [CO_2]
Low vpdL	High vpdL
Higher light intensities (PPFD)	Lower light intensities (PPFD)

The sensitivity of the reduction in g_s with increasing *vpdL* varies among plant species,[20, 21] and the net result is either a mitigated increase in E ,[22-26] or rarely, in some plants, E declines as g_s becomes severely reduced.[23,27-30] Any decline in g_s will also, to some degree, restrict A and growth, even in well-watered plants.[16,31] Reduced growth from increased *vpdL* occurs in herbaceous plants,[32-41] as well as shrubs and trees.[42-46] Water loss through E can also exacerbate whole-plant water stress, especially if combined with soil drying. As water becomes more difficult to pull from the soil, increasing demand through the leaves pulls at the water columns running throughout the vascular system. Gas bubbles (embolisms) can form and lead to disconnected water columns (cavitation).[47] Because of the interconnectedness of whole-plant water status, high *vpdL* is often combined with drought (soil drying) experiments.[48]

In contrast to the effects of high *vpdL*, potential limitations on plant growth from low *vpdL* are nutrient deficiency or impaired metabolism (Figure 2). Although it may be intuitive to think plants require some level of E to pull and maintain the flux of nutrients from the roots to the developing above-ground tissue, evidence is lacking to support this hypothesis; low E does not restrict nutrient uptake in sunflower (*Helianthus annua* L.) or *Arabidopsis*.[49,50] Regardless of whether low E is a contributing factor in tomato (*Solanum lycopersicum* L.), here a low *vpdL* can reduce the concentrations of calcium (Ca) and potassium (K) in the vegetative tissues. Reduced concentration of Ca and K can lead to some level of deficiency, which can lead to reduced growth.[51-55] Hybrid aspen (*Populus tremula* × *P. tremuloides*) also shows nutrient deficiency and reduced growth compared to untreated plants after several years of chronically lower *vpdL*, and here the reduced growth was linked to impaired metabolism.[56-58]

1.2.2 Traits that mitigate or exacerbate vpdL effects on plant growth

Plant traits can mitigate or exacerbate changes to g_{wv} (and E) that may result from a high or low *vpdL*. The leaf surface area to volume ratio (*SA:V*) moderates how E can transiently affect leaf water status. If the vascular system cannot hydraulically support leaves (eg. roots dry out), leaf *SA:V* can affect how quickly leaves dry out. Plants that evolved in the tropics or humid understory of temperate forests tend to have broad thin leaves with a high *SA:V*. As a result, these plants are more susceptible to drying out at higher *vpdL*, and are more sensitive to closing their stomata and restricting their growth (eg. banana (*Musa* spp.)). On the other end of the spectrum, plants that evolved in hot, arid environments tend to have leaves with a low *SA:V*, which are generally more resistant to drying out and have a greater water storage capacity (eg. cacti). Cacti and other succulents also tend to have stomata sunken into pits, having only small apertured pores exposed to the outside air, thereby chronically reducing g_{wv}. Plants that evolved in more temperate environments tend to have traits that fall somewhere between these two extremes.

Biochemical and anatomical modifications inside the leaf can also achieve greater rates of A at lower g_s, again mitigating the tradeoff between water loss through E and carbon gain through A. These biochemical and anatomical modifications are termed CO_2 concentrating mechanisms (*CCMs*), and include C_4 and Crassulacean Acid Metabolism (*CAM*) photosynthesis for higher plants. *CAM* plants open their stomata at night and close them during the day, when CO_2 is re-released from crassulacean acid formed during the night and concentrated around the site of CO_2 fixation. In this way *CAM* plants reduce water loss not only through suppressing photorespiration, but also by limiting gas exchange to nighttime when temperatures are cooler, thereby reducing E (Equation 7).[59] By concentrating CO_2 (and excluding O_2) around the site of CO_2 fixation through a C_4 cycle (inside specialized cells), C_4 plants eliminate photorespiration, which acts to decrease A in C_3 plants.[60] At higher *vpdL* that can reduce g_s, the drop in intercellular CO_2 concentration in C_3 plants exacerbates photorespiration, further reducing A relative to C_4 plants.[61] The active CO_2 pump in C_4 plants achieves greater A at lower g_s, and C_4 plants generally show lower g_s compared to ecologically similar C_3 plants when measured under the same conditions.[62, 63] As a result, E is also lower in C_4 plants, often resulting in greater water use efficiency of A compared to ecologically similar C_3 plants, often expressed as A/E.[22,23,63,64]

1.2.3 – A low vpdL may be beneficial or essential to your plant growth objectives

Through the same process that can cause nutrient deficiency, a low *vpdL* (low E) can also alleviate salt stress by reducing the uptake of toxic salts.[65-72] Maintaining a low *vpdL* is frequently required to grow vegetative cuttings, as often their underdeveloped root system cannot hydraulically support high rates of E from their relatively large leaf area. For Cannabis (*Cannabis* sp.), a recommended *vpdL* is 0.8 kPa for vegetative cuttings, steadily increasing with plant growth to 1.5 kPa for maturing flower buds.[73] A low *vpdL* can also increase leaf extension rate from improved leaf water status, thereby increasing light interception capacity and growth.[74] In sweet potato (*Ipomoea batatas* (L.) Lam.) and potato (*Solanum tuberosum* L.), reducing the *vpdL* from 1.2 to 0.4 or 1.9 to 0.6 kPa shifts biomass allocation to the edible tubers with little or no effect on overall growth (dry biomass).[75,76]

If plants grown at low *vpdL* are to be moved to an area of higher *vpdL*, take care to avoid humidity shock. Stomata of plants grown at low *vpdL* are acclimated to the humid air, and often cannot properly close in response to higher *vpdL*. As a result, leaf and plant water status decline, which can lead to more severe dehydration in some cases. If plants are to be moved from areas of low to high *vpdL*, gradually increase exposure to higher *vpdL* (over days) if possible to mitigate humidity shock.[77,78]

1.2.4 – A low vpdL can encourage infection from pathogens

Although growth at low *vpdL* may be beneficial to your goals, low *vpdL* can also encourage the incidence and severity of fungal and bacterial pathogens. The incidence and severity of powdery mildew (*Uncinula necator* (Schwein.) Burrill) infection on grape seedlings (*Vitis vinifera* L. cv 'Riesling') increases with decreasing *vpdL* until 0.5 kPa (85% *RH* at 25°C), where it plateaus or marginally decreases.[79] For other fungi such as *Cercospora carotae* (Pass.) Solheim, a pathogen of carrots (*Daucus carota* L. var. *sativa* Hoffm.), and *Magnaporthe* oryzae (B.C.) Couch, a pathogen of perennial ryegrass (*Lolium perenne* L.), a threshold *vpdL* must be achieved before infection occurs. For *C. carotae* this threshold is a range from 0.3 to 0.8 kPa (84% *RH* at temperatures from 16 to 32°C),[80] and for *M.*

oryzae the threshold is 0.3 kPa (92% *RH* at 28°C).[81] *Fusarium* sp. is a fungal pathogen of wheat (*Triticum aestivum* L.) that attacks the developing grain (known as fusarium head blight). Here two species (*F. avenaceum* and *F. graminearum*) appear to require condensation (0 kPa *vpdL*, 100% *RH*) at 30°C to achieve appreciable infection rates, whereas one species (*F. culmorum*) achieves its greatest infection rate at 1.5 kPa *vpdL*, (65% *RH* at 30°C), with declining infection rates at lower *vpdL*.[82] *Xanthomonas sp.* is a genus of bacterial pathogens, causing leaf spots, scabs, or cankers in peppers (*Capsicum annum* L.), tomatoes, and citrus trees (*Citrus* sp.).[83-85] In peppers, appreciable infection occurs at 0.7 kPa *vpdL* (85% *RH*) and increases down to 0 kPa *vpdL* (100% *RH*) at 30°C.[84] In tomatoes, 0.7 kPa *vpdL* (80% *RH*) caused 4.6 times more bacterial leaf spot lesions compared to 2.5 to 2.2 kPa *vpdL* (30 to 45% *RH*) at 27°C.[85]

1.2.5 – Vpd affects the longevity and viability of pollen and seeds

In some plants such as annual mercury (*Mercurialis annua* L.), hoary rock-rose (*Cistus x incanus* L.), and common myrtle (*Myrtus communis* L.), a low *vpd* can reduce the amount of time pollen remains viable after it is released, especially at temperatures >20°C.[86,87] In contrast, a high *vpd* can also reduce the amount of time pollen remains viable after it is released in the common poppy (*Papaver rhoeas* L.) and the European fan palm (*Chamaerops humilis* L.).[87] Lower *vpd* speeds up pollen metabolism and oxidative decay whereas higher *vpd* may dry pollen out. Long-term storage of viable pollen is best accomplished by rapid drying to a given *vpd* and immediate transfer and storage at ultra-low temperatures (-80°C freezer or liquid N_2 (-196°C)). Seeds are generally best kept at even higher *vpd* than pollen, and, depending on the species, can be kept viable in the fridge (4°C), -20°C freezer, or ultra-low temperatures (-80°C freezer or liquid N_2 (-196°C)).[88,89]

1.2.6 – A safe or optimal vpdL for plant growth is species specific

To understand how the *vpdL* may affect the growth of your plant species, first consider its morphology, anatomy, and the environment where it evolved or is bred to grow. Is your plant adapted to humid or dry climates or microclimates? Is your plant adapted to windy or calm climates or microclimates? Does your plant have a *CCM*? I.e. is it a C_4 (maize (*Zea mays* L.), sugarcane (*Saccharum* sp.), sorghum (*Sorghum bicolor* (L.) Moench), switchgrass (*Panicum virgatum* L.)) or *CAM* (pineapple (*Ananas comosus* (L.) Merr.), agave (*Agave* sp.)) plant? Most research and crop plants use C_3 photosynthesis, and in general, here *A* and growth are more sensitive to increasing *vpdL* compared to plants with *CCMs*. If your research relates to growth rate, nutrition, leaf growth (morphology), or stomatal size or density, think about how the *vpdL* may affect this research. If the goal is to compare your results to the literature, match the *vpdL* conditions if possible, and if not, use the discrepancies in growth conditions to help interpret any differences in the results. Keep in mind that for many plants, increasing the *vpdL* from 0.2 to 1.2 kPa has no significant effect on growth. This can be true for lettuce (*Lactuca sativa* L.), cucumbers (*Cucumis sativus* L.), and potato, among several others.[34,35,75] For other plants, increasing the *vpdL* from 0.2 to 2.8 kPa has little to no effect on *A*, including wild type *Arabidopsis thaliana* (L.) Heynh. (Columbia).[22,23,90]

If maximizing plant growth is your goal, decreasing the vpdL to <1 kPa can increase *A* and/or growth by 10 to 68% in some C_3 plants.[23,32-35,37,39,46,76,91] In potted plants, the potential nutrient limitation from low *vpdL* can likely be alleviated by increasing the fertilization regimen, as shown with *Begonia* sp..[92] Potted plants are more prone to nutrient deficiencies in general, but here you also have more control over their fertilization. As already discussed in a previous section, risks of growing plants at low *vpdL* include pathogen infection and humidity shock if plants are moved out of a low *vpdL* environment.

An optimal *vpdL* range to maximize plant growth is species specific and may be narrow or wide. Stepping outside this range may begin to show small or large effects on *A* or growth. What is considered to be a safe *vpdL* range may be subjective; many species may show some degree of growth restriction with increasing *vpdL* but are healthy and do not show any visible signs of stress. Online, many references to a safe or optimal *vpdL* range are for Cannabis, and this should not necessarily be interpreted as a safe or optimal range for all plant species. Once you have determined an acceptable *vpdL* range for your species, you can make a reference chart that indicates which temperatures and *RH* are required to stay in this range.

Here is a free *vpdL* calculator and chart maker to help keep you in a given range: https://pulsegrow.com/blogs/learn/vpd

Here is a free app to calculate other humidity related parameters: https://www.vaisala.com/en/lp/humidity-calculator

Part 2: Factors that add or remove water vapor inside growth chambers or rooms

Now that you've determined an acceptable *vpdL* range for plant growth, how do you determine whether you can achieve this? The following sections discuss how to estimate water vapor loads from plants (whole-plant *E*), how to adjust the *vpdL* in growth chambers without formal humidity control, factors that affect the ambient humidity of growth chambers, and how to interpret humidity control specifications.

2.1 – How to estimate water vapor loads from plants and their pots on a whole-plant or growth area basis

Potted plants and their wet soil emit water vapor into growth chambers and rooms. Estimating *E* on a whole-plant or growth area basis (E_{wp} or E_{ga}) may be desirable for scheduling the frequency of watering, estimating how much water to top up hydroponic systems, and estimating the flow rates of aeroponic misting systems.

Estimates of *E* rely on estimates of g_s for a given set of conditions (Equations 5 & 6). Because of the tradeoff between carbon gain through *A* and water loss through *E*, there is a strong relationship between *A* and g_s. This relationship has been empirically determined and modelled for a number of species, the Ball-Berry model (*BBM*) being one model that is widely used.[31] The *BBM* also incorporates *RH* and ambient [CO_2] in addition to *A* to determine g_s. At this point it is also important to calculate gas exchange parameters based on whether stomata are located on both the top and bottom of leaves (amphistomatous), only on the bottom of leaves (hypostomatous), or rarely only on the top of leaves (hyperstomatous).[93] To extend g_s to total leaf conductance to water vapor (g_{wv}), the average boundary layer conductance (g_{bl}) of leaves must be approximated (Figure 2).[2] Estimates of g_{wv} can then be used to calculate *E* (Equations 5 & 6). Next *E* can be scaled to E_{wp} or E_{ga}, the latter based on the average leaf area per unit ground area, often referred to as the leaf area index (LAI, m^2 leaf area m^{-2} ground area).[94] For large plants, if values of *A* for the *BBM* are from upper-most fully expanded leaves (which they often are), a scaling factor is also required to account for shading, leaf age, and light attenuation.[95] Finally to model *E*, certain assumptions are required about the *VP* of the air inside the growth chamber that is interacting with the plants.

In one scenario, *E* for sunflower is modelled with an ambient *VP* of 1.24kPa (21°C, 50% *RH*) across a range of temperatures (Figure 3). In Figure 4 the ambient *RH* is held at 50% across a range of temperatures, showing how *E* increases at lower temperatures, but is markedly reduced at warmer temperatures compared to Figure 3 (Figure 4 vs Figure 3). Herein lies a central challenge in estimating *E* and how much plants affect the *VP* inside growth chambers or rooms; more *E* increases the *VP* but a higher *VP* reduces *E*. This same effect occurs for lettuce (*Lactuca sativa* L.), but here note the lower values of *E* due to lower g_s (Figures 5 & 6). To estimate the upper limits of whole-plant *E* and water vapor loads inside growth rooms, we modelled sunflower under a max LAI of 3.5. This hypothetical growth room is filled with large sunflower plants under high light intensities. Here removing water vapor via dehumidification will be the challenge and we assumed *RHs* of 70% at 15°C, 65% at 20°C, 60% at 25°C, 55% at 30°C, and 50% at 35°C. Finally we can convert *E* to water vapor load units of kg hr^{-1} m^{-2} which are more readily used to size de-humidification equipment (Figure 7). This process can be applied to other crops such as lettuce, here assuming 50% *RH* across a

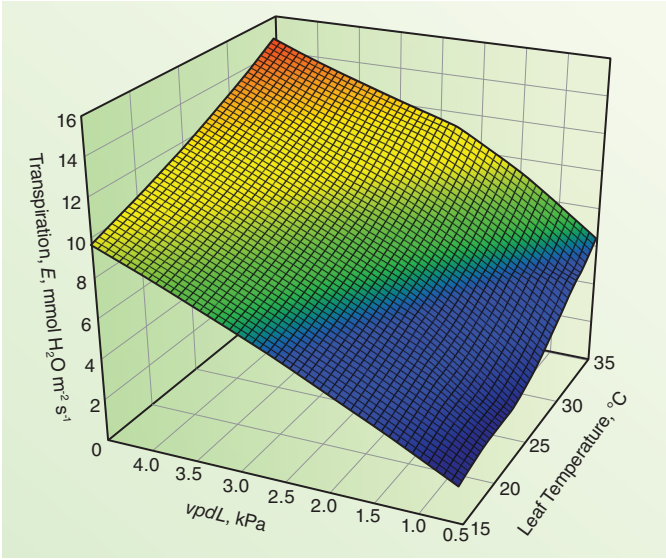

Figure 3: Modeled *E* (m^{-2} of leaf area) of sunflower across changing leaf temperatures and *vpdL*. In this example, **the air inside the growth chamber has a constant *VP* of 1.24 kPa** and leaf temperature is 1°C higher than air temperature. Values of *A* to estimate g_s with the Ball-Berry Model[31] were taken from Bunce, 2000.[96] Here *A* was measured across a range of leaf temperatures at 1500 *PPFD* and an ambient [CO_2] of 350 µmol mol^{-1} (ppm).[96] Slope (*m*) and intercept (g_0) values for the *BBM* were taken from Miner & Bauerle, 2017 (P1 of Figure 3).[97] Estimates of g_{bl} assumed an average leaf path vector of 10 cm (0.1 m) and air movement of 0.7 m s^{-1}. Total conductance to water vapor (g_{wv}) and *E* were calculated from Equations 6 & 5.[2,10]

range of temperatures (Figure 8). The water vapor loads are again lower with lettuce compared with sunflower, again due to lower g_s but also from a lower modelled LAI of 1 which is likely close to the upper limit for lettuce (Figure 8).

Another way to estimate *E* is to calculate the energy load from the light canopy and assume projected leaf area = floor/growth area. Here we converted light spectra and intensities (*PPFD*) to watts m^{-2} (not lamp watts) and used the heat of vaporization (at leaf temperature) to determine water vapor loads (Figure 9). This method assumes leaves behave like exposed water and does not consider g_{wv}.

Pot volume is an important determinant of overall plant size, and affects *E* through its overall effects on plant growth and leaf area[101,102] Pot volume and soil surface area also affect evaporation from the soil (S_{Evap}). For recently watered pots with soil that conducts water well, evaporation rates may be similar to a dish of water, with only boundary layer constraints, and can be estimated by: [2,103]

$$S_{Evap} = g_{wv}\,(W_{soil} - W_{air}) \qquad \text{(Equation 9)}$$

$$g_{wv} = g_{bl} \qquad \text{(Equation 10)}$$

As soil dries, it behaves less and less like a dish of water and rates of evaporation may be better estimated by:

$$S_{Evap} = st^{1/2} + bt \qquad \text{(Equation 11)}$$

Where *s* is sorptivity, *t* is time, and *b* is a constant (< 0).[103-106]

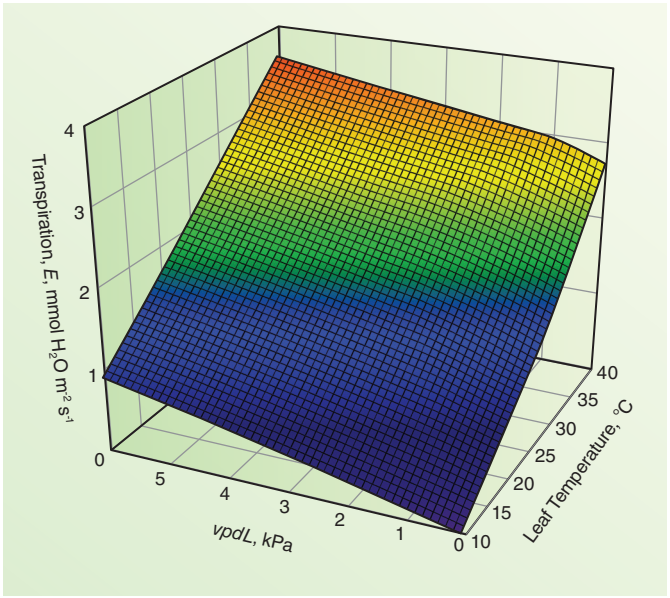

Figure 5: Modeled transpiration (*E*, m^{-2} of leaf area) of lettuce across changing leaf temperatures and *vpdL*. In this example, **the air inside the growth chamber has a constant *VP* of 1.24 kPa** and leaf temperature is 1°C higher than air temperature. Values of net CO_2 assimilation rates (*A*) to estimate stomatal conductance (g_s) with the Ball-Berry Model[31] were taken from Kim *et al.* 2004.[98] Here *A* was measured at 400 *PPFD* light intensity, 20°C, and an ambient [CO_2] of 600 µmol mol^{-1} (ppm).[98] Next, the relative change in *A* was estimated across leaf temperatures higher and lower than 20°C based on the average C_3 response of *A* to temperature from Yamori *et al.* 2014.[99] Slope (*m*) and intercept (g_0) values for the *BBM* were taken from Jung *et al.* 2016[100] and Kim *et al.* 2004[98] respectively. Estimates of boundary layer conductance assumed an average leaf path vector of 5 cm (0.05 m) and air movement of 0.7 m s^{-1}. g_{wv} and *E* were calculated from Equations 6 & 5.[2,10]

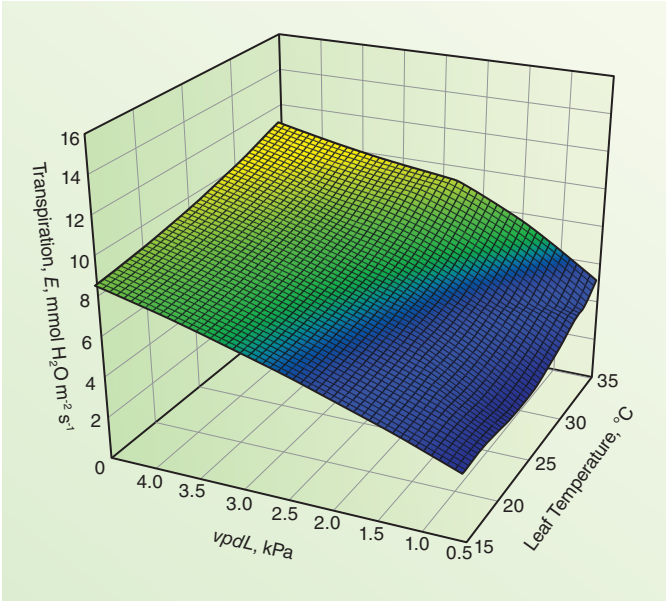

Figure 4: Modeled transpiration (*E*, m^{-2} of leaf area) of sunflower across changing leaf temperatures and *vpdL*. In this example, the air inside the growth chamber has a constant *RH* of 50% across all temperatures. All other models, values, equations, and assumptions are the same as Figure 3.

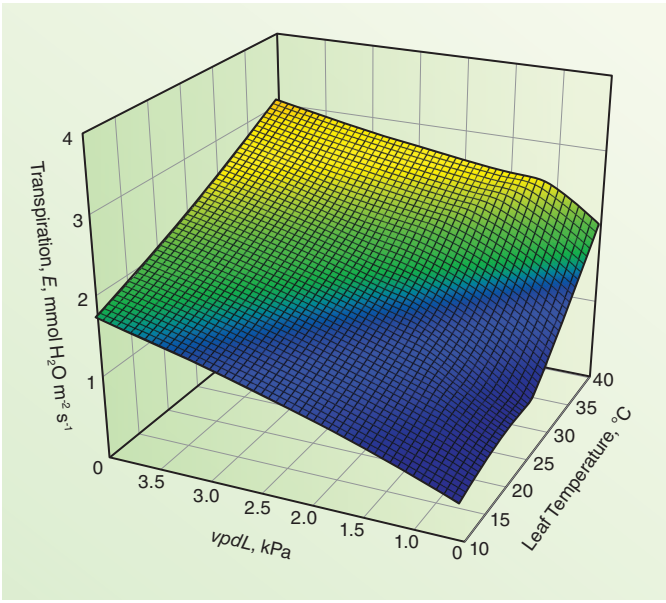

Figure 6: Modeled *E* (m^{-2} of leaf area) of lettuce across changing leaf temperatures and *vpdL*. In this example, the air inside the growth chamber has a constant *RH* of 50% across all temperatures. All other models, values, equations, and assumptions are the same as Figure 5.

2.2 How to adjust the vpdL in growth chambers without formal humidity control

Temperature and *RH* both indirectly and directly affect *E* through their effects on g_s and the *vpdL*. Temperature control in growth chambers and rooms is standard. Humidity control includes several options, and is often recommended depending on the application and where the equipment will be installed. **In growth chambers without formal humidity control, the *vpdL* can be manipulated by changing the temperature, adding or removing sources of water vapor, and/or adjusting the fresh air flow rate.** Lowering the temperature or adding more plants are two options to lower the *vpdL*. Overwatering, wetting a cloth with a large surface area, or installing a household humidifier are other ways to add sources of water vapor inside your existing growth chamber and lower the *vpdL* (please consult with your chamber manufacturer). Finally, with sources of water vapor inside growth chambers, reducing the fresh air flow rate will likely lower the *vpdL*, allowing the sources of water vapor inside to build up and concentrate. **However, be careful about reducing the fresh air flow too much, as the [CO_2] can potentially be reduced below ambient and slow plant growth. Ethylene and other volatiles can also build up with little fresh air flow, potentially causing undesirable growth effects, especially if chambers are filled with plants** (Figure 10).[107] With only a few small plants, the fresh air flow rate can often be reduced to lower the *vpdL* without appreciably affecting the [CO_2] inside a growth chamber or room. To increase the *vpdL*, increase the temperature, or in most situations with plants inside your growth chamber, increase the fresh air flow rate (Figure 10).

How fresh air flow affects the *vpdL* inside a growth chamber depends on the *VP* difference between the fresh air coming in and the air inside. The greater the difference in *VP*, the more fresh air will either reduce or increase the *vpdL*. In growth chambers filled with plants, in most cases fresh air will increase the *vpdL*, as the water vapor load from plants will raise the *VP* higher than the fresh air coming in. How much fresh air changes the *vpdL* also depends on its flow rate; the greater the fresh air flow rate the more fresh air will change (in most cases increase) the *vpdL* (Figure 10).

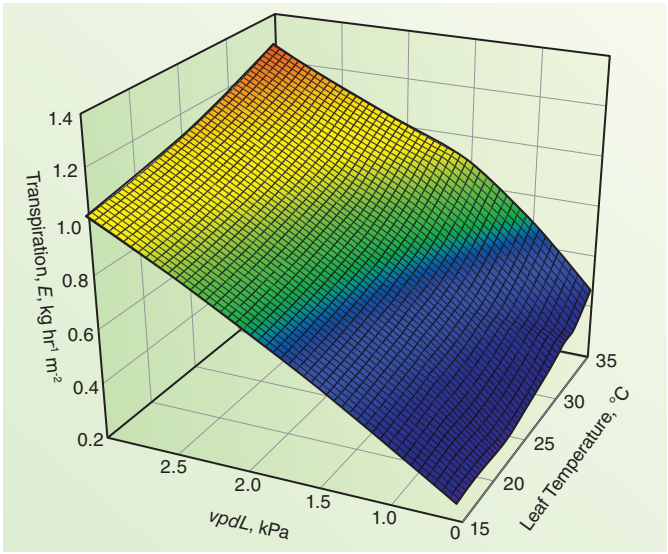

Figure 7: Estimated water vapor loads from sunflower (m^{-2} of growth area), assuming an LAI of 3.5. In this example, **the air inside the growth chamber has *RH*s of 70% at 15°C, 65% at 20°C, 60% at 25°C, 55% at 30°C, and 50% at 35°C**. *E* values were reduced by 50% after multiplying by 3.5 to account for shading and leaf age effects[95] before conversion to kg hr^{-1} m^{-2}. All other models, values, equations, and assumptions are the same as Figure 4.

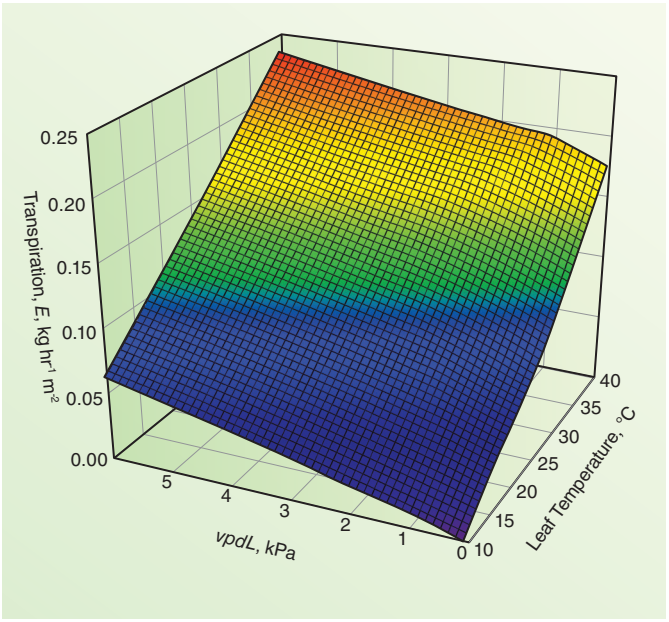

Figure 8: Estimated water vapor loads from lettuce (m^{-2} of growth area), assuming an LAI of 1. In this example, the air inside the growth chamber has a constant *RH* of 50% across all temperatures. This is a direct conversion of *E* values from Figure 6 to kg hr^{-1} m^{-2}.

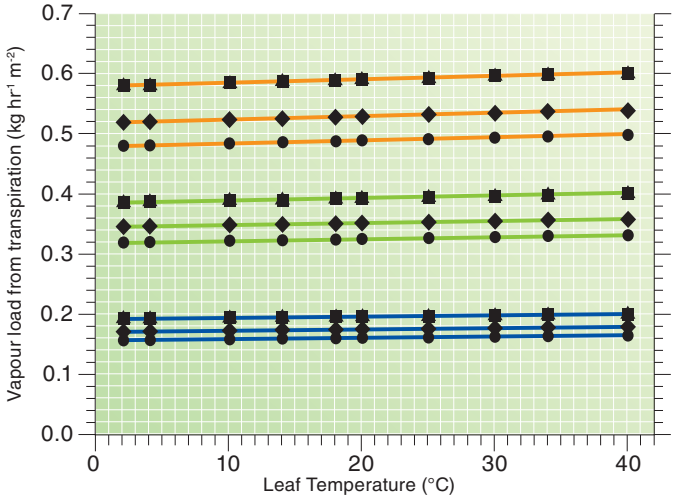

Figure 9: Calculated water vapor load from *E* as a function of leaf temperature. Here we converted light spectra and intensities (*PPFD*) to watts m^{-2} and used the heat of vaporization (at leaf temperature) to estimate water vapor loads. This method assumes projected leaf area = floor/growth area, that leaves behave like exposed water, and does not consider g_{wv}.
Blue lines = 500 PPFD. Green lines = 1000 PPFD. Orange lines = 1500 PPFD. Circles = white LED fixture. Diamonds = white, red, and far-red LED fixture. Squares = high-pressure sodium + metal halide bulbs. Triangles = fluorescent tubes + halogen bulbs.

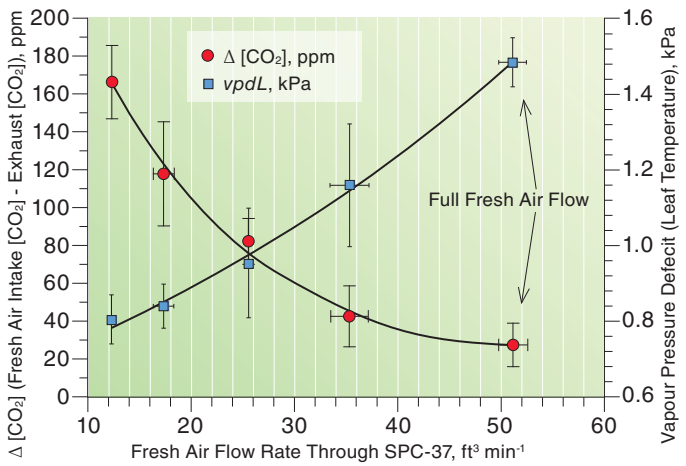

Figure 10: Drawdown of CO_2 concentration and change in the *vpdL* as a function of fresh air flow inside a BioChambers SPC-37. Here the growth chamber was filled with well-watered and fertilized maize and soybean plants. Leaf temperatures ranged from 25.5 to 26.5°C (chamber set-point 25°C) and *PPFD* averaged 430 µmol m^{-2} s^{-1} across the upper leaves. The LAI of all plants was 0.48. Flow rates were decreased by manually closing the fresh air intake valve from fully open (arrow). After each flow rate change, at least 45 minutes passed before measurements were recorded to allow for steady state conditions. The air outside the BioChambers building was an average of 2.5°C at 95% *RH* (0.69 kPa *VP*) over the course of measurements.[111] Mean ±SE.

The *VP* of the fresh air flowing into your growth chambers depends on the characteristics of the building(s) where the chambers are installed. How is the air conditioned and circulated inside your building? What are the sources of water vapor and how well is your building sealed? Where in the world are you located? What time of year is it? In buildings without humidity control, geographic location and time of year can be the prevailing factors in determining the *VP*s of the ambient fresh air. Latitudinally, the greatest average (annual) *VP*s occur near the equator and follow a bell-curve toward the poles.[3] There is also significant variation in *VP*s longitudinally, for example from east of the Sierra Nevada mountain range to the east coast of the USA.[108] Time of year also changes the *VP* of air, with summers generally having higher *VP*s than winters. For example, if we compare the average *VP* of Winnipeg, Manitoba, Canada in January (0.16 kPa) with Tallahassee, Florida, USA in July (2.76 kPa) and bring them both to 21°C, we see a *vpdL* of 2.37 kPa (6% *RH*) for Winnipeg and *vpdL* of 0 (>100% *RH*) for Talahassee.[109,110] If we compare average *VP*s of Winnipeg in summer (July) (1.61 kPa) with winter (January) (0.16 kPa) at 21°C, we see a *vpdL* of 0.88 kPa (65% *RH*) for July and 2.37 kPa (6% *RH*) for January.[110] Here without additive humidity in your chamber, during the winter, there could be significantly different seasonal growth responses. Figure 11 shows how dry the air can be in Winnipeg in winter when warmed up to 30°C inside a BioChambers TPC-19. Here, adding four maize plants linearly reduces the *vpdL* from 4.2 to 3.9 kPa. However, a 3.9 kPa *vpdL* will reduce *A* and growth to some degree in the majority of plants compared to lower *vpdL*. Compare Figure 11 with a BioChambers SPC-37 filled with maize and soybean (*Glycine max* (L.) Merr.) plants at 25°C, also in Winnipeg in late fall (Figure 10). Here, the *vpdL* ranges from 1.5 to 0.8 kPa as the fresh air flow is reduced. The differences between these tests (at full fresh air flow) are the amount of plant material, a 5°C temperature difference, and the greater *VP* of the ambient fresh air coming into the SPC-37 (Figures 10 & 11).

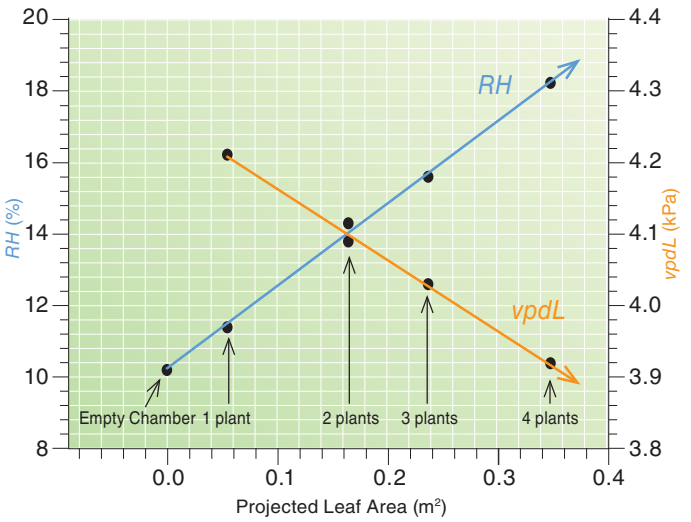

Figure 11: How *RH* and the *vpdL* change by adding well-watered and fertilized maize plants (projected leaf area) to a BioChambers TPC-19 growth chamber. Here the chamber was at full fresh air flow, leaf temperatures were 31.5°C on average (chamber set-point 30°C, and *PPFD* averaged 650 µmol m^{-2} s^{-1} across the upper leaves. The air outside the BioChambers building was an average of -19.4°C at 75% *RH* (0.16 kPa *VP*) over the course of the measurements.[112]

2.3 Formal options to control humidity and the vpdL inside growth chambers

2.3.1 Additive humidity

Spray nozzle additive humidity is the most popular and cost effective option to lower the *vpdL*. Spray nozzle additive humidity increases the *RH* by running pressurized water through a spray nozzle, emitting small water droplets that evaporate into the air. Remember that increasing the *RH* (reducing the *vpdL*) is more challenging at higher temperatures, as warmer air "holds" more and more moisture (Figure 1). A typical specification for spray nozzle additive humidity may look something like this:

"Up to 75% *RH* with all lights on, up to 90% *RH* with all lights off, and limited by a 25°C *DPT*. Based on ambient fresh air of 21°C at 50% RH (1.24 kPa *VP*)."

The specification states that the equipment can maintain 75% *RH* (lights on) or 90% *RH* (lights off) or higher, at temperatures equal to or lower than a 25°C *DPT* (ie. the *SVP* of 25°C). This means at around 27°C or lower you can maintain 90% *RH* and at 30°C or lower you can maintain 75% *RH*. Keep in mind this specification assumes ambient fresh air enters the growth chamber at 21°C at 50% *RH* (1.24 kPa *VP*) at full fresh air flow. The realized performance of the equipment will depend on the condition of the actual ambient fresh air and how much plant material is inside. Plant material adds water vapor, so if the ambient air is at 21°C at 50% *RH* (1.24 kPa *VP*), adding plant material may increase the additive humidity capabilities of your equipment.

Ultrasonic additive humidity is more expensive but uses water more efficiently and does not require a high pressure water supply. Ultrasonic additive humidity works by generating ultrasonic pulses through water columns to generate very small micro droplets (<1 micrometer diameter) which rapidly evaporate into the air. A specification for ultrasonic additive humidity is interpreted the same way as spray nozzle additive humidity. To prevent build-up of mineral deposits that can clog these additive humidity systems, relatively clean water is required. Either de-ionized, reverse osmosis, or distilled water is acceptable, and must be supplied at 60 to 100 psi pressure for the spray nozzle option.

2.3.2 De-humidification

De-humidification by refrigeration is a popular and cost-effective way to add some de-humidification capacity to equipment. With this option, the conditioned air inside the chamber is run over the cool evaporator coil of the refrigeration equipment to condense out some water vapor before re-entering the growth area. This is the same principle as the condensation drip often seen on the back of window air conditioners. In contrast to additive humidity, reducing the *RH* or increasing the *vpdL* is more challenging at lower temperatures, which "hold" less water vapor and saturate at lower *VP*s. A typical specification for de-humidification by refrigeration looks like this:

"Down to 45% *RH* with all lights on or off and limited by an 8°C *DPT*. Based on ambient fresh air of 21°C at 50% *RH* (1.24 kPa *VP*)."

This specification means that this equipment can maintain 45% *RH* or lower at temperatures equal to or greater than an 8°C *DPT* (ie. the *SVP* of 8°C), which is around 21°C or higher. Again, this specification assumes a water vapor load of ambient fresh air entering the equipment at 21°C at 50% *RH* (1.24 kPa *VP*) at full fresh air flow. In contrast to additive humidity, adding plants and other sources of water vapor will decrease de-humidification capacity.

De-humidification through desiccant drying is more expensive than by refrigeration, but achieves appreciably greater de-humidification capacities. Here, the conditioned air inside the chamber passes through a drying wheel with a chemical desiccant that is continually regenerated with heat. Because desiccant dryers come in several sizes/capacities, estimating the water vapor load from fresh air and plants is important to help size the desiccant dryer only to the specification you need, as the cost differences between drying units are significant. A specification for de-humidification through desiccant drying is interpreted the same way as de-humidification by refrigeration, where a lower limiting *DPT* means a greater capacity to de-humidify.

Appendix 1

Temperature, °C	Saturation Vapour Pressure (SVP), kPa
-10	0.259
-9	0.283
-8	0.310
-7	0.338
-6	0.368
-5	0.401
-4	0.437
-3	0.476
-2	0.517
-1	0.562
0	0.611
1	0.657
2	0.706
3	0.758
4	0.816
5	0.873
6	0.935
7	1.002
8	1.073
9	1.148
10	1.228
11	1.313
12	1.403
13	1.498
14	1.599
15	1.706
16	1.819
17	1.938
18	2.064
19	2.198
20	2.339
21	2.488
22	2.645
23	2.810
24	2.985
25	3.169
26	3.363
27	3.567
28	3.782
29	4.008
30	4.246
31	4.495
32	4.758
33	5.034
34	5.323
35	5.627
36	5.945
37	6.280
38	6.630
39	6.997
40	7.381
41	7.784
42	8.205
43	8.646
44	9.108
45	9.590

Appendix 2 - List of abbreviations:

VP: Vapor pressure, kPa

SVP: Saturation vapor pressure, kPa

RH: Relative humidity, %

DPT: Dew point temperature, °C, corresponds to a *SVP*

vpd: Vapor pressure deficit of the air, kPa

vpdL: Vapor pressure deficit between leaves and the air, kPa

E: Transpiration rate, mmol H2O m^{-2} (leaf area) s^{-1}

A: Net CO_2 assimilation rate, µmol CO_2 m^{-2} s^{-1}

g_{wv}: Total leaf/plant conductance to water vapor, mmol H_2O m^{-2} (leaf area) s^{-1}

g_s: Stomatal conductance to water vapor, mmol H_2O m^{-2} (leaf area) s^{-1}

g_{bl}: Boundary layer conductance to water vapor, mmol H2O m^{-2} (leaf area) s^{-1}

PPFD: Photosynthetic photon flux density, µmol photons (400-700nm) m^{-2} s^{-1}

SA:V: Surface area to volume ratio

CAM: Crassulacean acid metabolism

E_{wp}: Whole-plant transpiration rate, mmol H_2O m^{-2} (leaf area) s^{-1}

E_{ga}: Whole-plant transpiration rate, mmol H_2O m^{-2} (growth area) s^{-1} (with a given LAI) Or, kg H2O hr^{-1} m^{-2} (growth area, with a given LAI)

LAI: Leaf area index, m^2 leaf area m^{-2} growth area

BBM: Ball-Berry model of stomatal conductance[31]

CCM: CO_2 concentrating mechanism

S_{evap}: Evaporation rate from the surfaces of soil in pots, mmol H_2O m^{-2} s^{-1}

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