`tdllicor`
R-package documentation

Erik B. Erhardt David T. Hanson

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Contents

Chapter 1

Install and execute

1.1 Install software

R and Perl are required. Rstudio may make your experience more enjoyable.

1. R (requires R 2.15.1+)
   (a) Windows (`http://cran.r-project.org/bin/windows/base/`) or
   (b) Mac (`http://cran.r-project.org/bin/macosx/`)
2. Rstudio
   (a) Rstudio (`http://www.rstudio.org/download/`) nicer GUI
3. Perl
   (a) Mac and linux, you already have it installed
   (b) Windows
      i. `http://www.activestate.com/activeperl/downloads`
      ii. Change the path variable to include `C:\Perl\bin` (or whatever it is on your machine, and use backslashes): `http://www.java.com/en/download/help/path.xml`

1.2 Install the `tdllicor` package

Install the tdllicor package From the shared dropbox folder `./TDL_R_scripts/` install the current version of tdllicor. The package installation file will appear in a folder named something like

- `./tdllicor_0.1-21_20121017-R2.15.1-template4/`

and will include two files, such as

- the package: `tdllicor_0.1-21.tar.gz`
- and the template: `tdllicor_template4.xls`

There doesn't seem to be a way to install local packages within R anymore, so it has to be done from the command prompt. From your shell or command prompt:

1. Windows, open your command prompt (cmd), change to directory with install file, and install it (you need to get the correct path, filename, and R command name).
   (a) `cd C:\[your path]\TDL_R_scripts\tdllicor_0.1-21_20121017-R2.15.1-template4`
   (b) `"C:\Program Files\R\R-2.15.1\bin\x64\R" CMD INSTALL tdllicor_0.1-21.tar.gz`
2. Mac, I can't walk you through this since I don't have access to a Mac right now, but it's similar, probably something like this:
   (a) `cd ~/[your path]/TDL_R_scripts/tdllicor_0.1-21_20121017-R2.15.1-template4`
   (b) `R CMD INSTALL tdllicor_0.1-21.tar.gz`

Copy the template file to your data directory before you rename and edit it.

1.3 Analyze your TDL and/or Licor data with `tdllicor`

Try to avoid using spaces in your directory names (folder names) and file names.

Analyze your TDL and/or Licor data

1. Create a new data analysis directory, such as `./Name_WT001`
2. Copy your TDL and Licor files into your new dir
3. Copy the `tdllicor_template4.xls` into your new dir
4. Append a meaningful suffix to the `.xls` file, such as `tdllicor_template4_Name_WT001.xls`
5. Edit the `.xls` file and specify the TDL and Licor filenames, and make any other necessary changes to template inputs.
6. Load the library: (see end of doc for the remaining steps all together)
   (a) `library(tdllicor)`
7. Assign the xls filename to a variable
   (a) `input.fn <-"tdllicor_template4_Name_WT001.xls"`
8. Specify your new dir (using forward slashes for all systems is preferred)
   (a) Mac, Linux:
      i. `path <-"/Users/username/Analysis/Name_WT001"`
   (b) Windows:
      i. `path <-"C:/Dropbox/Analysis/Name_WT001"`

9. Run the analysis
    (a) a. `tdllicor(input.fn, path)`
10. It will create an `./out` directory where output files are created.
11. Documentation is available with `?tdllicor`

Use a block of code like this, set your file name and directory, and copy/paste into R.

```
library(tdllicor)
# ?tdllicor
input.fn <- "tdllicor_template4_Name_WT001.xls"
path <- "/Users/username/Analysis/Name_WT001" # Mac
path <- "C:/Dropbox/Analysis/Name_WT001"      # Windows
tdllicor(input.fn, path)
```

Chapter 2

Calculations

2.1 Gas exchange calculations

2.1.1 Constants

While each of these values have their own associated uncertainty, we take them to be constant at their (accepted) values for an analysis. Common values are included below, though these may be changed in the template.

$\dot{a}_{\text{b}} \equiv 2.96‰$ boundary
$\dot{a} \equiv 4.44‰$ stomata
$\dot{a}_{\text{w}} \equiv 0.7‰ \equiv \dot{a}_{\text{l}}$ water
$\dot{b}_{\text{s}} \equiv 1.1‰$ CO2 entering solution at 20°C
$\dot{b} \equiv 29‰$ internal conductance via gm
$\dot{R}_{\text{std 13C}} \equiv 0.0111797$ C ratio of standard
$\underset{\sim}{\dot{\kappa}}_{\text{H}} \equiv (\dot{\kappa}_{\text{H12}}, \dot{\kappa}_{\text{H13}})^\top \equiv (473.3358029, 5.183209292)^\top$ concentration constants for high tanks
$\underset{\sim}{\dot{\kappa}}_{\text{L}} \equiv (\dot{\kappa}_{\text{L12}}, \dot{\kappa}_{\text{L13}})^\top \equiv (243.4737846, 2.666301131)^\top$ concentration constants for low tanks
$\dot{f}_{\text{13C}} \equiv 0.004922$ natural fractional abundance of C isotopologues not measured
$\dot{g}_{\text{bc}} \equiv 3$ conductance at the boundary level, can also be obtained from Licor

2.1.2 Data

TDL

Concentrations for high and low calibration tanks (H and L), reference gas entering the chamber (R), and chamber gas exiting the chamber (C).

$\underset{\sim}{\tilde{\kappa}}_{\text{H}} = (\tilde{\kappa}_{\text{H12}}, \tilde{\kappa}_{\text{H13}})^\top$
$\underset{\sim}{\tilde{\kappa}}_{\text{L}} = (\tilde{\kappa}_{\text{L12}}, \tilde{\kappa}_{\text{L13}})^\top$
$\underset{\sim}{\tilde{\kappa}}_{\text{R}} = (\tilde{\kappa}_{\text{R12}}, \tilde{\kappa}_{\text{R13}})^\top$
$\underset{\sim}{\tilde{\kappa}}_{\text{C}} = (\tilde{\kappa}_{\text{C12}}, \tilde{\kappa}_{\text{C13}})^\top$

Licor

$\tilde{p}_{\text{atm}} \sim \text{Normal}(p_{\text{atm}}, \sigma^2_{p_{\text{atm}}})$ atmospheric pressure from Licor
$\tilde{A} \sim \text{Normal}(A, \sigma^2_A)$ photosynthesis from Licor (can also calculate from TDL)

$\tilde{g}_{\mathrm{tc}} \sim \mathrm{Normal}(g_{\mathrm{tc}}, \sigma^2_{g_{\mathrm{tc}}})$ total conductance of CO_2 (I have a note that this is a function of $\dot{g}_{\mathrm{bc}}$, $\dot{g}_{\mathrm{sc}}$, $\dot{a}_{\mathrm{b}}$, $\dot{g}_{\mathrm{sc}}$, and $\dot{g}_{\mathrm{bc}}$.)

$\tilde{E} \sim \mathrm{Normal}(E, \sigma^2_E)$ transpiration rate (water vapor)

2.1.3 Calculations

Concentration

Offset

$o_{12} = \dot{\kappa}_{\mathrm{H12}} - g_{12}\kappa_{\mathrm{H12}}$

$o_{13} = \dot{\kappa}_{\mathrm{H13}} - g_{13}\kappa_{\mathrm{H13}}$

Gain

$g_{12} = (\dot{\kappa}_{\mathrm{H12}} - \dot{\kappa}_{\mathrm{L12}})(\kappa_{\mathrm{H12}} - \kappa_{\mathrm{L12}})^{-1}$

$g_{13} = (\dot{\kappa}_{\mathrm{H13}} - \dot{\kappa}_{\mathrm{L13}})(\kappa_{\mathrm{H13}} - \kappa_{\mathrm{L13}})^{-1}$

Corrected

$\kappa'_{\mathrm{R12}} = \kappa_{\mathrm{R12}}g_{12} + o_{12}$ Ref

$\kappa'_{\mathrm{R13}} = \kappa_{\mathrm{R13}}g_{13} + o_{13}$ Ref

$\kappa'_{\mathrm{C12}} = \kappa_{\mathrm{C12}}g_{12} + o_{12}$ Chamber

$\kappa'_{\mathrm{C13}} = \kappa_{\mathrm{C13}}g_{13} + o_{13}$ Chamber

xi

$\xi = C_{\mathrm{e}}(C_{\mathrm{e}} - C_{\mathrm{o}})^{-1}$

delta

$\delta_{\mathrm{e}} = \{(\kappa'_{\mathrm{R13}}/\kappa'_{\mathrm{R12}})/\dot{R}_{\mathrm{std\ 13C}} - 1\}10^3‰$ Ref

$\delta_{\mathrm{o}} = \{(\kappa'_{\mathrm{C13}}/\kappa'_{\mathrm{C12}})/\dot{R}_{\mathrm{std\ 13C}} - 1\}10^3‰$ Chamber

Total mol fractions (paired, either both Licor or both TDL)

$C_{\mathrm{e}} = (\kappa'_{\mathrm{R12}} + \kappa'_{\mathrm{R13}})(1 - \dot{f}_{\mathrm{13C}})^{-1}$ entering Reference

$C_{\mathrm{a}} \equiv C_{\mathrm{o}} = (\kappa'_{\mathrm{C12}} + \kappa'_{\mathrm{C13}})(1 - \dot{f}_{\mathrm{13C}})^{-1}$ outgoing Chamber

2.1.4 Partial Pressures

$p_{\mathrm{a}} = (C_{\mathrm{a}}10^{-6})(p_{\mathrm{atm}}10^3)$ atmosphere

$p_{\mathrm{s}} = (C_{\mathrm{s}}10^{-6})(p_{\mathrm{atm}}10^3)$ surface

$p_{\mathrm{i}} = (C_{\mathrm{i}}10^{-6})(p_{\mathrm{atm}}10^3)$ internal

$p_{\mathrm{c}} = p_{\mathrm{i}} - Ag_{\mathrm{m}}^{-1}$ (chloroplast) carboxylation site

$g_{\mathrm{m}} = (\dot{b} - \dot{b}_{\mathrm{s}} - \dot{a}_{\mathrm{w}})Ap_{\mathrm{a}}^{-1}(\Delta_{\mathrm{pred}} - \Delta_{\mathrm{obs}})^{-1}$

Discrimination

(can put priors here, if desired)

$\Delta_{\mathrm{obs}} = \xi(\delta_{\mathrm{o}} - \delta_{\mathrm{e}})\{1 + \delta_{\mathrm{o}} - \xi(\delta_{\mathrm{o}} - \delta_{\mathrm{e}})\}^{-1}10^3$

$\Delta_{\mathrm{pred}} = p_{\mathrm{a}}^{-1}\{\dot{a}_{\mathrm{b}}(p_{\mathrm{a}} - p_{\mathrm{s}}) + \dot{a}(p_{\mathrm{s}} - p_{\mathrm{i}}) + \dot{b}p_{\mathrm{c}}\}$

(circular, assume $p_{\mathrm{c}} \equiv p_{\mathrm{i}}$)

Leaf surface:

$C_{\mathrm{s}} = \{(\dot{g}_{\mathrm{bc}} - E/2000)C_{\mathrm{o}} - A\}(\dot{g}_{\mathrm{bc}} + E/2000)^{-1}$

$C_{\mathrm{i}} = \{(g_{\mathrm{tc}} - E/2000)C_{\mathrm{o}} - A\}(g_{\mathrm{tc}} + E/2000)^{-1}$

Either of these valuse can be from the TDL or Licor: C_{o} and A.

2.2 Discrimination and (photo)respiration

We are interested in estimating the amount of respiration e and photorespiration f for each genotype and condition using the comprehensive model. In the Bayesian paradigm, all model parameters are random and informed by data and prior information, or are defined in terms of other parameters. Inference for model parameters is based on the posterior joint probability distribution function (pdf) of all the parameters given all the data and prior information, though the structure of the posterior may often be simplified by considering the conditionality structure of the parameters.

2.2.1 Background

Illuminated leaves simultaneously assimilate (gross photosynthetic assimilation) and produce (photorespirat and day respiration) CO_2. While photosynthesis is a building process, photorespiration is a breaking-down process where photosynthesis is effectively running in reverse. Photorespiration is a wasteful process because it produces waste ammonia that must be detoxified at a substantial cost to the cell in ATP (energy) and reducing equivalents. Potential photosynthetic output may be reduced by photorespiration by up to 25% in C3 plants (Sharkey, 1988). Unlike photosynthesis and photorespiration, respiration does not depend on light, so it occurs at night as well as during the day and generally thought to be regulated independently of processes in the light.

While the general metabolic scheme of the respiratory pathway is known, the regulation of day respiration (respiration occurring during daylight hours) is one conundrum of plant photosynthetic biology. In fact, day respiration is the cornerstone for nitrogen assimilation by leaves simply because carbon assimilation produces organic materials (carbohydrates) that are in turn converted to nitrogen acceptors by respiration. This process is also thought to be influenced by photorespiration, potentially resulting in modified, non-cyclic respiratory pathway in leaves. Unsurprisingly then, intense efforts are currently devoted to elucidate the metabolic basis of the regulation of day respiration and photorespiration, with the optimization of nitrogen assimilation for a better yield of crop plants as an ultimate goal. Thus, the development of a statistical model appropriately accounting for sources of uncertainty and prior information will have broad application in understanding photosynthetic pathways and carbon usage in plants.

2.2.2 Research questions to be addressed

1) What are the rates of day respiration e (mitochondria) and photorespiration f (ribisco grabs 1 O_2 and attaches to sugar, WT takes relases 2 CO_2 and PMDH releases 4 CO_2 via phtorespiration) and the isotopic signature of the CO_2 they release? 2) What is the uncertainty of our estimations of day respiration and photorespiration rates? 3) Are rates of photorespiration and day respiration linked? 4) How much uncertainty do these estimates contribute to measures of photosynthetic parameters?

2.2.3 Strategy

Analysis procedures The proposed model development and analysis procedures will comprise four phases carried out over one semester and summer (6 months).

Phase 0, Data has already been collected For the initial data collection (already done), we use a combined tunable diode laser (TDL) infrared gas analizer system developed by Barbour et al.

(2007) to measure the exchange of $^{13}CO_2$ and $^{12}CO_2$ between leaves and the air provided to them. The physical and biochemical processes leading to the differential assimilation of each isotopelogue are well defined, but the processes that release CO2 from the leaf back into the atmosphere are not. The two primary sources of CO2 are respiration and photorespiration. We can separate these by conducting gas exchange in low oxygen (2%) environments that inhibit photorespiration and compare these to measurements made under ambient oxygen (21%). The difference in isotopic exchange between these conditions will represent the photorespiratory release. We can then get a respiration signal in (alluminator?) leaves by making measurements at two temperatures because the temperature response of photosynthesis and respiration are known and they differ. By modeling the photosynthetic exchange in two temperatures and the associated isotopic effects and comparing them to the measured changes we can calculate respiratory effects by calculating the difference between the modeled and measured values.

Phase 1, Frequentist (bootstrap) modeling The functional form of measurable and theoretical parameters will be written into a model. A prototype frequentist bootstrap estimation framework will be developed for estimating (photo)respiration subject to variability from measureable parameters. Using existing data from Dave Hanson we will fit the model using the plug-in principle. The plug-in principle is used when the underlying distribution for the sampling distribution of a parameter is unknown and a best guess is substituted for what that distribution is. For most sampling distributions we will substitute univariate normal distributions, and estimate the distributional parameters (mean and variance) from the observed sample. Then, the Monte Carlo strategy will be used to draw a large number (10^6) of samples from the estimated parametric distribution. In this way, parameters we can estimate directly with uncertainty are used to infer parameters we can not, while correctly accounting for the uncertainty in the inferred parameter (Davison and Hinkley, 1997). This model has the advantage of computational simplicity, relative to the Bayesian model in Phase 2.

Phase 2, Bayesian modeling The Bayesian estimation framework will extend the frequentist framework from phase 1. This model estimates non-fixed parameters conditional on the data and all the other parameters. This model also incorporates prior information on parameters, so that prior belief about each parameter may be informed from previous studies. The model will be fit and compared to the frequentist framework in Phase 1. Sensitivity analyses will be conducted to assess the effect of the priors on the posterior inference. This model has the advantage of including prior information, jointly estimating the parameters, and a probabilistic interpretation, but at the costs of higher required statistical expertise and computational demands. This model represents the best estimation that can currently be done.

Phase 3, Experiment Using experimental design methodology, a parsimonious, realizable, and powerful experiment will be designed allowing all parameters to be estimated (avoiding confounding). Data collected with tunable diode laser (TDL) and Licor instruments under these designed gas conditions will be used to inform the model parameters (from Phases 1 and 2) regarding (photo)respiration (Table 2.1 and Figure 2.1. This experiment will supplement the existing data used in Phases 1 and 2. Custom software will preprocess the TDL and Licor data (Erhardt and Hanson, 2012).

Phase 4, Validation Finally, we will use (photo)respiration-related data published in other studies as prior information in our model to inform estimates we observe in our experiment. In principle, our estimates will reflect the best information available (similar to a well-done meta-analysis). We will provide discussion of the practical points regarding model fit, diagnostics, and implementation of the model to guide usage by plant physiologists.

Experimental design The experiment is designed to estimate all model parameters well and to isolate respiration e and photorespiration f from each other. We record measurements under 6 controlled conditions by varying the gas characteristics flowing through a leaf chamber (Figure 2.1) high CO_2 (1000ppm), ambient CO_2 (400ppm), and low O_2 (2%), each at two reference isotope ratios $\delta = +148‰$ and $-4‰$ (Table 2.1). For each condition, 3 plants each of model organism *Arabidopsis thaliana* wildtype (WT) and mutants lacking peroxisomal malate dehydrogenase (PMDH) genotypes are each measured 3 times. There are a total of $108 = 6 \times 2 \times 3 \times 3$ multivariate observations.

The conditions specified in Table 2.1 allow us to estimate the rate parameters in the following way. It is assumed that e and f are independent. It is assumed that e is constant under the different CO_2 and O_2 conditions. Under low O_2 (conditions 5 and 6) it is assumed that $f \equiv 0$, so e can be estimated. The contrast between ambient and low O_2 (3 and 4 versus 5 and 6) allows estimation of f. High CO_2 (conditions 1 and 2) should decrease the overall rate of (photo)respiration, thus an additional parameter λ can be estimated for this proportion reduction. The large difference between the -4 and $+148$ δ conditions allows precise estimation of these parameters.

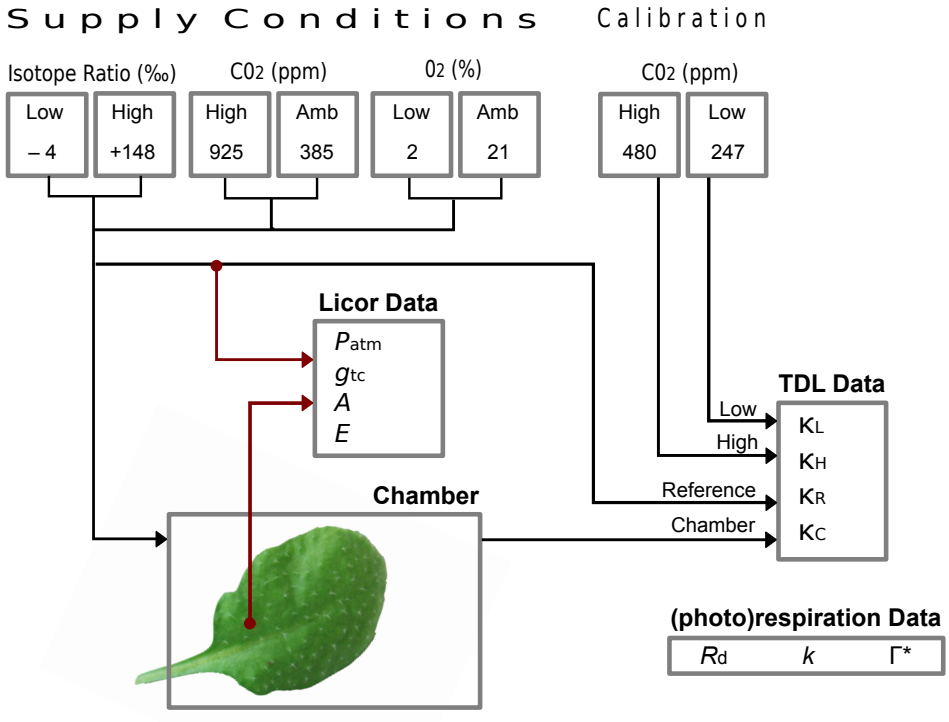

Figure 2.1: Schematic of the experimental configuration.

				Type ($t = 1, 2$)			
Cond	δ	CO_2	O_2	WT	PMDH	Purpose	Estimate
$c = 3$	+148	Hi(1000ppm)	Amb(21%)	3	3	reduced f	λ: $(1-\lambda)f$
4	−4	Hi(1000ppm)	Amb(21%)	3	3	reduced f	λ: $(1-\lambda)f$
5	+148	Amb(400ppm)	Amb(21%)	3	3	baseline	$f + e$
6	−4	Amb(400ppm)	Amb(21%)	3	3	baseline	$f + e$
7	+148	Amb(400ppm)	Low(2%)	3	3	$f \equiv 0$	e
8	−4	Amb(400ppm)	Low(2%)	3	3	$f \equiv 0$	e

Table 2.1: **Experiment.** For each of 6 conditions and 2 genotypes, 3 plants are measured.

2.2.4 Comprehensive model for discrimination

Farquhar's comprehensive model for discrimination (2.1) includes terms for respiration e and photorespiration f (Farquhar and Sharkey, 1982; Farquhar and Richards, 1984). By conducting controlled experiments that precisely estimate the other model parameters and that isolate when respiration and photorespiration are active we can make inference on e and f.

$$\begin{aligned}\Delta_{\text{comp}} &= p_{\text{a}}^{-1}\big[\dot{a}_{\text{b}}(p_{\text{a}} - p_{\text{s}}) + \dot{a}(p_{\text{s}} - p_{\text{i}}) + (\dot{b}_{\text{s}} + \dot{a}_{\text{w}})(p_{\text{i}} - p_{\text{c}}) + \dot{b}p_{\text{c}} \\ &\qquad - \big\{eR_{\text{d}}k^{-1} + f\Gamma^*\big\}\big]\end{aligned} \tag{2.1}$$

Frequentist (bootstrap) methods solve for and estimate an approximate sampling distribution for the (photo)respiration parameters by drawing samples from the estimated sampling distributions of the other parameters. The Bayesian approach estimates the posterior joint probability density function (pdf) of all these parameters conditional on data and prior information providing inference for all parameters.

Illustration of bootstrap method To understand the intuition behind the bootstrap method, let's see how to estimate an intermediate pressure parameter, p_{a}. The basic structure is that each parameter depends on a combination of constants (fixed and assumed known), sampling distributions of parameter estimates informed by data, or other parameters. Thus, all parameters are ultimately informed by constants or data.

First we define notation. Let "dot", $\dot{x}$, indicate a constant, "tilde", $\tilde{x}$, indicate data, and "undertilde", $\underset{\sim}{x}$, indicate a vector. The four subscripts are c=condition (1, 2, 3, 4, 5, 6; Table 2.1), t=genotype (1=WT, 2=PMDH), p=plant number (1, 2, 3), and r=repetition (1, 2, 3).

This pressure term, $p_{\text{a}} = (C_{\text{a}}10^{-6})(p_{\text{atm}}10^3)$, depends on a concentration (C_{a}) and the atmospheric pressure (p_{atm}). The atmospheric pressure from is measured from the Licor instument, and we assume that the observed data follow a normal distribution for which we estimate the mean and variance from the sample data, $\tilde{p}_{\text{atm}} \sim \text{Normal}(p_{\text{atm}}, \sigma^2_{p_{\text{atm}}})$. The concentration of CO_2 in the chamber depends on the corrected concentration of ^{12}C and ^{13}C and a constant, $C_{\text{a}} \equiv C_{\text{o}} = (\kappa'_{\text{C12}} + \kappa'_{\text{C13}})(1 - \dot{f}_{\text{13C}})^{-1}$. The constant is the fraction of C isotopologues not measured, $\dot{f}_{\text{13C}} \equiv 0.004922$. The corrected concentrations depend on the observed concentrations, as well as calibration gain and offset values, $\kappa'_{\text{C12}} = \kappa_{\text{C12}}g_{12} + o_{12}$ and $\kappa'_{\text{C13}} = \kappa_{\text{C13}}g_{13} + o_{13}$. The offset depends on constatnts, the gain, and the observed concentrations. The known concentration constants for high and low calibration tanks are $\dot{\underset{\sim}{\kappa}}_{\text{H}} \equiv (\dot{\kappa}_{\text{H12}}, \dot{\kappa}_{\text{H13}})^\top \equiv (473.3358029, 5.183209292)^\top$ and $\dot{\underset{\sim}{\kappa}}_{\text{L}} \equiv (\dot{\kappa}_{\text{L12}}, \dot{\kappa}_{\text{L13}})^\top \equiv$

$(243.4737846, 2.666301131)^\top$. The gain depends on constants and observed concentrations, $g_{12} = (\dot{\kappa}_{\mathrm{H}12} - \dot{\kappa}_{\mathrm{L}12})(\kappa_{\mathrm{H}12} - \kappa_{\mathrm{L}12})^{-1}$ and $g_{13} = (\dot{\kappa}_{\mathrm{H}13} - \dot{\kappa}_{\mathrm{L}13})(\kappa_{\mathrm{H}13} - \kappa_{\mathrm{L}13})^{-1}$. Finally, we assume that the observed concentrations follow a bivariate normal distribution for which we estimate the mean and covariance from the sample data, $\tilde{\underset{\sim}{\kappa}}_{\mathrm{H}} \sim \mathrm{Normal}(\underset{\sim}{\kappa}_{\mathrm{H}}, \Sigma_{\underset{\sim}{\kappa}_{\mathrm{H}}})$ and $\tilde{\underset{\sim}{\kappa}}_{\mathrm{L}} \sim \mathrm{Normal}(\underset{\sim}{\kappa}_{\mathrm{L}}, \Sigma_{\underset{\sim}{\kappa}_{\mathrm{L}}})$.

Each parameter has a similar chain of dependencies. The bootstrap draws samples from the sampling distributions and the series of parameter relationships are used to make inference on parameters of interest, including the uncertainty associated with all other parameters.

The posterior joint pdf of all these parameters conditional on data and priors provides inference for all parameters.

While Δ_{comp} is intended for making predictions, in the current experiment it estimates what is observed, Δ_{obs}. Therefore, we set $\Delta_{\mathrm{comp}} \equiv \Delta_{\mathrm{obs}}$.

Respiration and photorespiration

For simplicity, let the pressure terms be

$$\pi \equiv \dot{a}_{\mathrm{b}}(p_{\mathrm{a}} - p_{\mathrm{s}}) + \dot{a}(p_{\mathrm{s}} - p_{\mathrm{i}}) + (\dot{b}_{\mathrm{s}} + \dot{a}_{\mathrm{w}})(p_{\mathrm{i}} - p_{\mathrm{c}}) + \dot{b}p_{\mathrm{c}}.$$

The comprehensive model may be written as

$$p_{\mathrm{a}}\Delta_{\mathrm{obs}} = \pi - (eR_{\mathrm{d}}k^{-1} + f\Gamma^*).$$

Solving for e and f, we obtain

$$\begin{aligned} e' &= (\pi - p_{\mathrm{a}}\Delta_{\mathrm{obs}} - f\Gamma^*)(R_{\mathrm{d}}k^{-1})^{-1} \\ f' &= (\pi - p_{\mathrm{a}}\Delta_{\mathrm{obs}} - eR_{\mathrm{d}}k^{-1})(\Gamma^*)^{-1} \end{aligned}$$

where we let our observed values each be distributed normally:

$$\begin{aligned} e' &\sim \mathrm{Normal}(e, \sigma_e^2) \quad \text{and} \\ f' &\sim \mathrm{Normal}(f, \sigma_f^2). \end{aligned}$$

(priors for e and f)

These (photo)respiration parameters are currently estimated in another way **(why)**, and are taken as plant-level estimates each with a condition/genotype-specific mean and common variance.

Rd is estimated as 0.5 of the dark respiration and assumed to be independent of condition.

k and Γ^* are each estimated from other datasets, so we take them as input as data to this model.

$$\begin{aligned} \tilde{R}_{\mathrm{d}} &\sim \mathrm{Normal}(R_{\mathrm{d}}, \sigma^2_{R_{\mathrm{d}}}) \\ \tilde{k} &\sim \mathrm{Normal}(k, \sigma_k^2) \\ \tilde{\Gamma}^* &\sim \mathrm{Normal}(\Gamma^*, \sigma^2_{\Gamma^*}) \end{aligned}$$

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