

# Unravelling the phenology-phylogeny tangle.

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## Results & Discussion

Most analyzed species were sensitive to all three environmental cues—i.e., forcing, chilling, and photoperiod (Figs. 1, Supporting Table ??). Cue sensitivity led to phenological advances of 7.2 days per unit of standardized chilling, 5.8 days per unit of forcing, and 1.4 days/standard unit of photoperiod (see Table ??), on average. These average sensitivities to cues vary widely across species with larger variation found in responses to chilling, then to forcing and very little variation in how species respond to photoperiod (Figs. 1, Supporting Table ??). Overall, these findings coincide in their ranking of cue importance with previous ones (Ettinger et al., 2020) and advise against traditionally cross-species modelling schemes where one single cue sensitivity (i.e., slope) is forced to suit all species.

Our results reveal how responses to cues greatly differ among clades. For example, oaks and beeches (Fagaceae), elms (Ulmaceae) and buckthorns (Rhamnaceae) are highly sensitive to chilling while rhododendrons (Ericaceae), butterfly bushes (Scrophulariaceae) or spindles (Celastraceae) show little to no response to chilling (Fig. 1 a). A similar clade-level variation is found for forcing, where some of these clades—e.g., Ericaceae, Rhamnaceae, Ulmaceae, or Fagaceae—are particularly sensitive (advancing their budburst more than 10 days per standardized unit of forcing) and others such as the Sapindaceae, Cornaceae or Juglandaceae families show little response (Fig. 1 b).

Considering more than one cue, some clades are highly sensitive to two cues at the same time, which would suggest the existence of syndromes where the genetic basis for responses to one cue (e.g., forcing) could have been selected for along responses to another cue (e.g. chilling). However, clade-level responses to multiple cues are significantly but weakly correlated ( $r = 0.31$ ; between forcing and chilling) as responses to chilling are more variable and, the relationship among responses is non-linear (see Supporting Information XX). Weak correlations likely reflect how other clades such as *Tilia* and Ericaceae display strong responses to forcing but weak responses to chilling, or how genera such as *Betula* and *Populus* show strong intra-clade differences in their responses to chilling (Fig. 1). Interestingly, whichever the type, phenological responses to cues show structuring at the clade level that could have an evolutionary imprint in the phylogeny.

Our modelling approach allows to explicitly test whether there is phylogenetic structuring in how species respond to environmental cues. Phylogenetic signal as measured by our ‘phylogenetic shrinkage parameter’ ( $\lambda$ ) differs markedly across cues (Fig. 3). Tree phenological responses to environmental cues were strongly phylogenetically clustered for forcing ( $\lambda = 0.65$ ), moderately so for chilling ( $\lambda = 0.54$ ) and weakly for pho-

toperiod ( $\lambda = 0.39$ ) (see Fig. ??, Table ??). Sensitivity to photoperiod treatments did not vary across clades while responses to forcing are more variable across species and tend to be similar among closely related species (Fig. 1). Results showing that phylogenetically close species tend to show similar responses to some cues but not others, support the need to account for phylogeny in multi-species, multi-predictor modelling of phenological responses to cues.

Along evolution, tree species would have been constrained in their ability to develop responses to forcing that differ much from those of their close relatives, and somewhat less constrained in their responses to chilling. In contrast, responses to photoperiod seem evolutionarily labile, with little variation across most species (0.86 days per standard unit of photoperiod) and a few exceptions from the genus *Fagus*, known as particularly sensitive to photoperiod (Fu et al., 2019). Specifically, *Fagus sylvatica* is nearly five times more sensitive to photoperiod than most tree species. The question arises as to whether species with outlying responses should be chosen as the model from which to extrapolate knowledge as done with *Fagus sylvatica* in the phenology literature (REFs for PEP75?!).

Why would distantly related species respond more similarly and less variably to photoperiod than they do to forcing or chilling? Clearly, daylength is a more 'reliable' cue in temperate latitudes, as it varies (and has varied) less than forcing or chilling both across years and along evolutionary time. As such, it would have enabled species scheduling their phenological events to match most suitable environmental conditions (Jackson, 2009). The adaptation to shifting daylength may have occurred very early in the evolution of photoperiodic sensing—i.e., as early as in cyanobacteria (Hut and Beersma, 2011; Serrano-Bueno et al., 2017). If responses to photoperiod had evolved early in plants and kept more or less constant afterwards in absence of novel selective advantages—i.e., consistent with an Early Burst model of evolution—that would be consistent with our pattern of little variation in the responses to photoperiod across species and clades. Such degree of variation would be measured by our cue-level  $\sigma$  parameter, and is significantly smaller for photoperiod than for other cues. We run simulation tests that show how our results for photoperiodic responses would be consistent with the outcome of an Early Burst model of evolution (see Appendix XXX).

Not accounting for phylogeny had an effect on model coefficients (model slopes for forcing and chilling shifted by 7.2% and 3.7%, respectively; Fig. 4) and shifted cross-species variance in their responses to forcing ( $\text{Var } \beta_{\text{phylo}} = 8.74$ ;  $\text{Var } \beta_{\text{non-phylo}} = 5.01$ ), chilling ( $\text{Var } \beta_{\text{phylo}} = 23.45$ ;  $\text{Var } \beta_{\text{non-phylo}} = 17.47$ ), and photoperiod responses ( $\text{Var } \beta_{\text{phylo}} = 0.82$ ;  $\text{Var } \beta_{\text{non-phylo}} = 0.93$ ). Counterintuitively, induced reductions in cross-species variance, far from increasing estimation accuracy could lead to increased type-II error by failing to detect

actual relationships among cue and responses that would only emerge when phylogeny is accounted for (see Supporting Information XX). Assuming phylogenetic structuring to follow a Brownian Model of evolution (fixing  $\lambda = 1$ ) biased model coefficients too (model slopes for forcing and chilling shifted by 20.5% and 11.8%, respectively; Fig. 4). Either ignoring ( $\lambda = 0$ ) or overestimating phylogenetic structuring of predictors ( $\lambda = 1$ ) can bias model coefficients (predictors with high  $\lambda$  are biased in non-phylogenetic models and those with low  $\lambda$  are biased if Brownian Motion is imposed). Importantly, not accounting for phylogeny increased the uncertainty around each individual species estimation of their responses to forcing and chilling (see Fig. SXX in Supporting Information), which could lead to less precise predictions and forecasts of phenology for individual species although overall model accuracy would not be compromised (see Appendix XX in Supporting Information).

Accurate forecasts of phenology remain elusive, partly due to recent records of declines in species phenological sensitivity to increasing temperatures (Fu et al., 2015; Piao et al., 2017)—although such declines could derive from statistical artifacts (Wolkovich et al., 2021). Whatever the case, tests of declines in phenological sensitivity to warming will rely in accurate estimation of responses to cues, and we show here that such estimations are improved by accounting for their phylogenetic structuring. The need to incorporate phylogenetic information into the phenology research programme has long been acknowledged (Davis et al., 2010; Davies et al., 2013; Joly et al., 2019), to a point where it makes whole new research programme. Papers on this topic are mostly grounded on findings of non-random phylogenetic signal in both phenological traits (Davies et al., 2013; Rafferty and Nabity, 2017) and phenological responses to cues (Davies et al., 2013; Joly et al., 2019). Our approach differs from previous research in that it estimates simultaneously the complex and non-stationary responses of each species to each cue (allowing slopes to vary across species; see (Davies et al., 2019)), and a metric of phylogenetic signal for each environmental cue driving phenological sensitivity. Doing so sheds light on how responses to cues have been configured along evolutionary time.

Identifying strong patterns in clade-level responses to cues may open (at least for clades with the strongest signal) a venue for predicting phenological sensitivities in unmeasured species. Imputation must be done with extreme care (Molina-Venegas et al., 2018), but would allow expanding the short list of plant species for which forecasting phenology is feasible. This is particularly true in the context of temperate woody plant species, for which we have multiple experimental observations at varying treatment levels for major well-known drivers of phenology. Further, our results reinforce the idea that ecological forecasting could move beyond using functional groups (e.g., IREFS) or even species complexes (e.g. Ettinger et al. (2020)), to making predictions for individual species, with improved forecasting abilities thanks to incorporating phylogenetic structuring in individual species responses to cues.

Ultimately, phylogenetic hierarchical models such as those used here, have the potential to inform which clades will be more sensitive to different climate shifts—e.g., changes in cold temperatures over winter or in warm temperatures in spring and summer—or, which clades emerge as particularly sensitive to cues only after phylogeny is accounted for. For example, oaks (genus *Quercus*) would not be amongst the most sensitive ones to forcing and chilling in non-phylogenetic models (see e.g., (Ettinger et al., 2020)), but its species gain sensitivity (2 days per standard unit of forcing and 4 days per standard unit of chilling, on average) through our models. In contrast, hierarchical non-phylogenetic models can constrain species level estimates in a way that is not useful as they (i) induce significant bias in estimated model coefficients, (ii) decrease variability in cross-species biological responses and, (iii) increase uncertainty around estimates of individual species sensitivity to cues. Together, our results indicate that either ignoring the phylogeny or imposing stronger phylogenetic relationships than actual ones would compromise model ability to generate accurate inference and prediction, which are increasingly needed in a warming world.

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## Tables and Figures

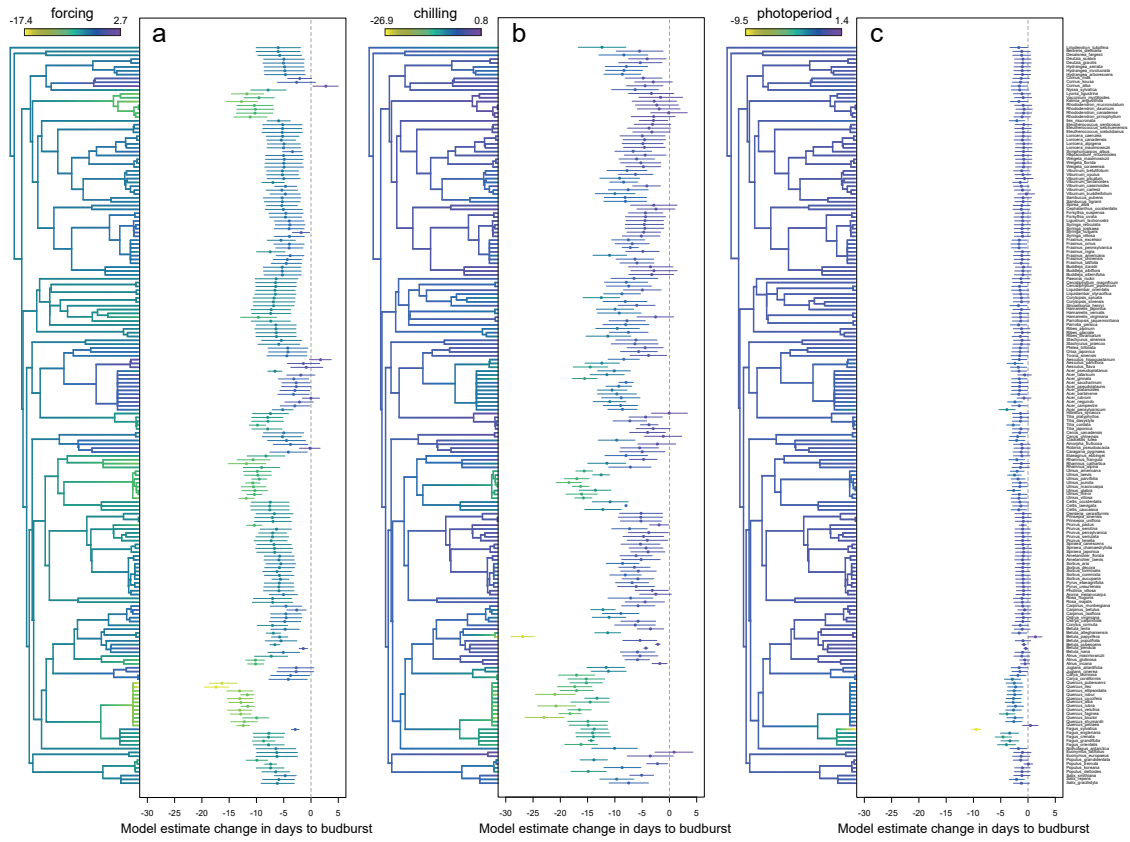


Figure 1: Phenological sensitivity to three environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 192 angiosperm species. The same phylogenetic tree is shown in each panel, colored according to an estimation of ancestral character states, being the states at the tips the model slopes of our hierarchical phylogenetic model. Note that the color scale varies in each panel. Total tree depth is 81. My.

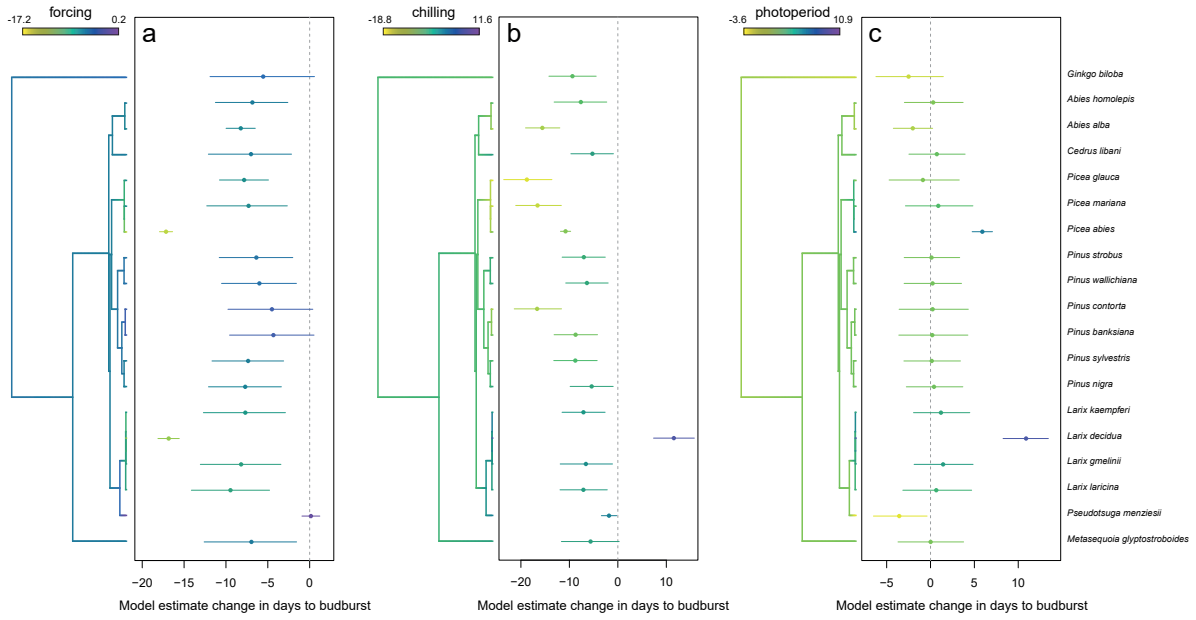


Figure 2: Phenological sensitivity to three environmental cues, forcing (a), chilling (b) and photoperiod (c) measured in change in days to budburst per standardized unit (z-transformation) of the cues across 19 gymnosperm species. The same phylogenetic tree is shown in each panel, colored according to an estimation of ancestral character states, being the states at the tips the model slopes of our hierarchical phylogenetic model. Note that the color scale varies in each panel. Total tree depth is 81. My.



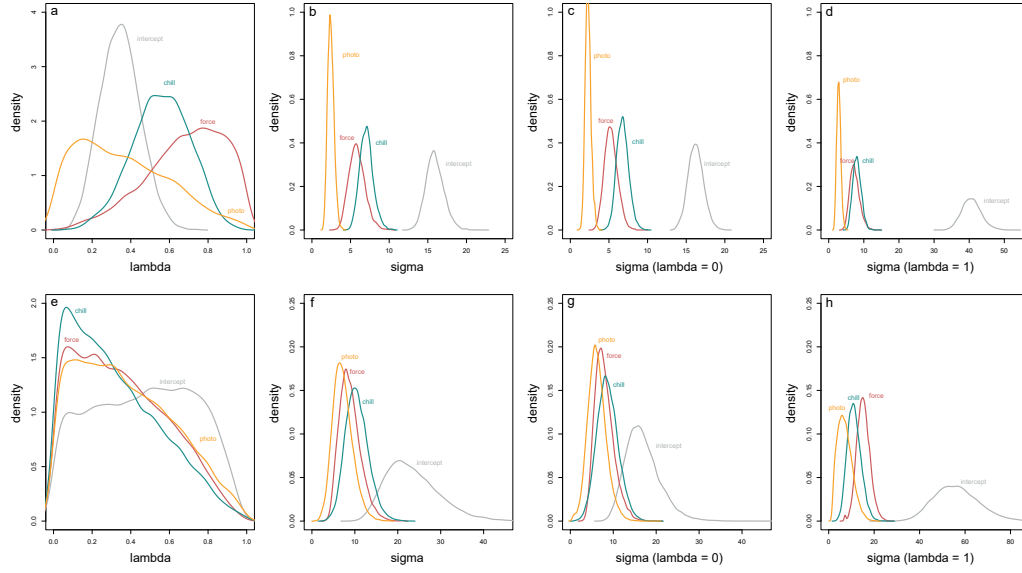


Figure 3: Density plots for the posterior distribution of phylogenetic signal measured by  $\lambda$  for each cue included as a predictor in the model for angiosperms: forcing (red), chilling (blue), photoperiod (orange) and for the model intercept (grey). Panels correspond to angiosperms (a-d) and gymnosperms (e-h). Note that  $\lambda$  estimations corresponding to panels c-d and g-h as they are constrained to be either equal zero or equal 1.

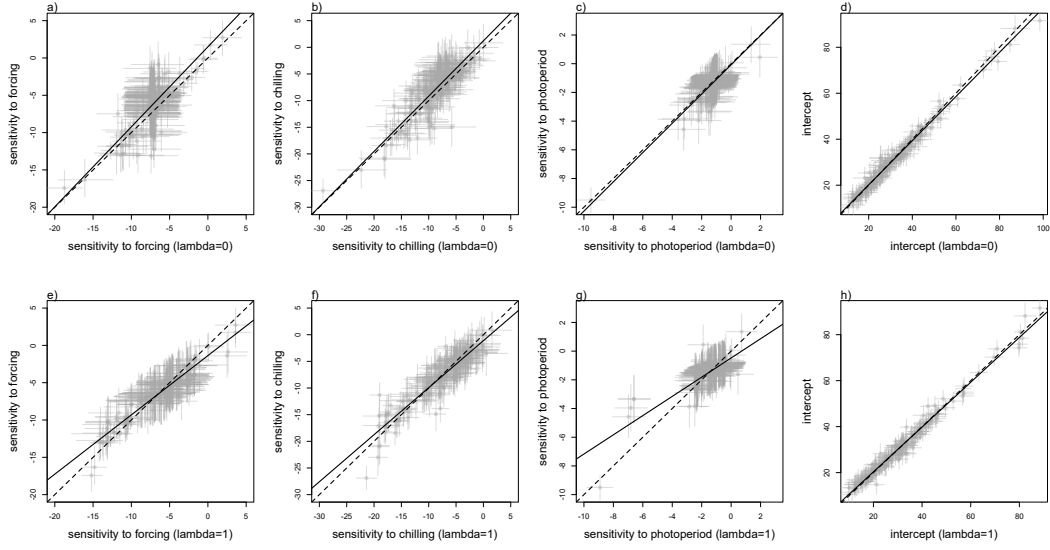


Figure 4: Correlations between model parameters as estimated by the full model and the models where  $\lambda$  is constrained to be equal zero (upper row) or one (bottom row), for angiosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

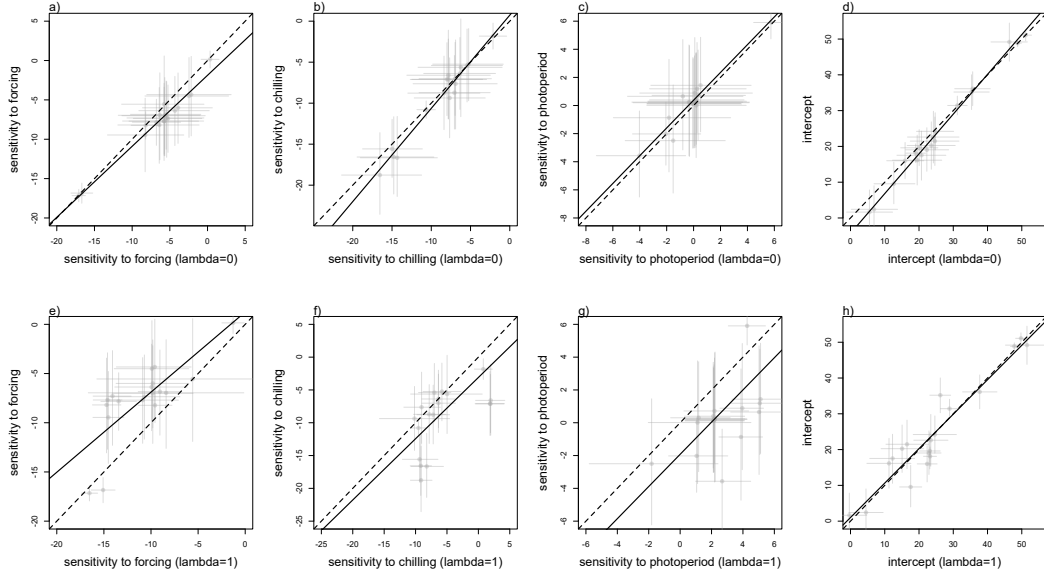


Figure 5: Correlations between model parameters as estimated by the full model and the models where  $\lambda$  is constrained to be equal zero (upper row) or one (bottom row), for gymnosperms. Panels correspond to sensitivity to forcing (a,e), to chilling (b,f), to photoperiod (c,g) and to model intercepts (d,h).

Table 1: Full model parameters estimated for 192 angiosperm species.

<b>parameter</b>	<b>mean</b>	<b>sd</b>	<b>2.50%</b>	<b>50%</b>	<b>97.50%</b>	<b>n_eff</b>
$\mu_\alpha$	30.57	3.41	23.68	30.59	37.14	5031.19
$\mu_{\beta forcing}$	-5.84	2.01	-9.72	-5.89	-1.79	2374.73
$\mu_{\beta chilling}$	-7.19	2.03	-11.15	-7.18	-3.18	3694.93
$\mu_{\beta photoperiod}$	-1.37	0.76	-2.92	-1.35	0.14	1565.41
$\lambda_\alpha$	0.35	0.10	0.16	0.34	0.56	3416.51
$\lambda_{\beta forcing}$	0.68	0.20	0.23	0.71	0.98	185.35
$\lambda_{\beta chilling}$	0.56	0.15	0.25	0.56	0.83	738.57
$\lambda_{\beta photoperiod}$	0.36	0.24	0.02	0.33	0.88	296.51
$\sigma_\alpha^2$	15.93	1.17	13.84	15.85	18.41	2988.37
$\sigma_{\beta forcing}^2$	5.84	1.04	4.03	5.78	8.15	502.74
$\sigma_{\beta chilling}^2$	7.05	0.87	5.48	7.02	8.92	1026.77
$\sigma_{\beta photoperiod}^2$	2.45	0.41	1.74	2.42	3.32	469.46
$\sigma_y^2$	12.81	0.18	12.47	12.80	13.17	4017.16

Table 2: Full model parameters estimated for 19 gymnosperm species.

<b>parameter</b>	<b>mean</b>	<b>sd</b>	<b>2.50%</b>	<b>50%</b>	<b>97.50%</b>	<b>n_eff</b>
$\mu_\alpha$	25.75	4.50	16.88	25.73	34.73	33151.86
$\mu_{\beta forcing}$	-5.92	3.80	-12.97	-6.05	1.90	16443.03
$\mu_{\beta chilling}$	-8.11	3.63	-15.31	-8.09	-0.94	21379.81
$\mu_{\beta photoperiod}$	-0.88	3.33	-8.01	-0.67	5.19	16301.93
$\lambda_\alpha$	0.47	0.26	0.02	0.48	0.90	15934.03
$\lambda_{\beta forcing}$	0.36	0.23	0.02	0.33	0.84	14336.60
$\lambda_{\beta chilling}$	0.32	0.23	0.01	0.28	0.82	13230.88
$\lambda_{\beta photoperiod}$	0.37	0.24	0.02	0.34	0.88	11199.49
$\sigma_\alpha^2$	23.47	6.20	13.87	22.59	37.81	18272.58
$\sigma_{\beta forcing}^2$	8.89	2.45	4.96	8.60	14.51	8126.51
$\sigma_{\beta chilling}^2$	10.47	2.66	5.78	10.30	16.17	8539.38
$\sigma_{\beta photoperiod}^2$	7.18	2.29	3.29	6.96	12.25	5625.69
$\sigma_y^2$	15.81	0.41	15.04	15.81	16.63	28640.16