

According to Issue #9;

Refs that show models where: models infer parameters (e.g., optimal chill) from other data or studies, then fit only certain parameters of their models to a dataset at hand. I have Richardson 1974, but there MUST be many more.

1. Can't find richardson1974 right now, but since chillingms.tex says:

Some of the early models from peaches, which underlie many of today's models, used experimental data of percent leaf or flower burst as evidence that chilling has been met then attempted to identify the range of temperatures where chilling accumulates \citep{erez1971}. Taking these estimated temperatures, they then used field observations of percent flowerburst for plants across a wide range of climates---including those well outside the natural range where percent flower burst in many years was low---to estimate the total chilling needed for different cultivars \citep{richardson1974}.

And also this:

One way to increase the amount of data used to estimate chilling models would be to include both experimental and observational data together in one model, but this has never been done to our knowledge. Instead, models continue to infer parameters from other data or studies, then fit only certain parameters of their models to a dataset at hand \citep{richardson1974}. While conditions in observational and experimental are often different---for example, many experiments apply cold temperatures in the dark, while photoperiod shifts each day in observational data---continually fitting the resulting data separately slows progress towards a coherent model and contributes to the increasing diversity of proposed models today.

2. So if X paper took the data from the Erez *et al.* series of papers on growing peaches but in some other country instead (like from the Mediterranean to the US, which I think is exactly what happened, like in the Utah Model??) and built a model out of this (like, chill units or chill time etc.). Then, as in richardson1974; "taking these estimated temperatures...used field observations of percent flower burst...to estimate the total chilling needed for different cultivars", where:

- a. "estimated temperatures" = the model built in a prior paper, in this case erez1971
- b. "Field observations" = current paper or a prior paper's empirical data
- c. "Estimate the total chilling" = applying said model from a prior paper to a whole new study system, then generating their own model outcomes

3. Any papers that come to mind with this kind of system?

- a. Overcash & Campbell (1955): explicit use of Weinberger (1950)'s peach cultivar chilling requirement model;

The two varieties chosen were Sunhigh with a short chilling requirement; and Redhaven, with a long chilling requirement. Weinberger...states that Sunhigh needs 750 hours of chilling at 45 degrees F or lower to break the rest period...Redhaven requires 850 hours for flower buds and 950 hours for leaf buds...at Fort Valley, Georgia.

This paper used intermittent warming to show that it could disrupt chilling accumulation (for lack of a better word, given the understanding of chilling at the time);

Both 750 and 950 hours of intermittent chilling were not totally effective in breaking the rest of either Redhaven or Sunhigh, because some of the symptoms of prolonged dormancy are displayed.

And fortunately, Overcash & Campbell (1955) also links to Bennett (1950) which did a similar experiment with hardy pear, and indeed this paper is the one which sparked the whole optimal chill temp clown fiesta. It also links to Weinberger (1954) which used the 'Sullivan Elberta' peach cultivar and found similar results of intermittent warming. There's also;

The effectiveness of high air temperatures and consequently higher twig temperatures on bright, sunny days in counteracting a certain amount of the chilling influence of lower temperatures is offered as a partial explanation of prolonged dormancy in Texas by Denman. (referring to Denman (1954))

- b. Fuchigami et al. (1982) looks promising because they outline in intense detail the definitions and parameters of their own model (the degree growth stages model) and, in each section, have papers that are relevant or support the development of this model (and they credit some of its structure to Sarvas (1973; 1974). This one is long though and needs some digesting...but it seems promising for a later bullet point in this issue?
- c. The model of apple bud development in Landsberg (1974) is built basically from scratch using empirical data, so it may be worthwhile to scan for papers that cite Landsberg (1974) in the creation of their own models or when they apply it to another study system

As a side note, Rageau *et al.* (1998) talks about 4 previously established conditions (things like temperature ranges, durations, etc.) and tests them to check their validity; maybe only tangentially related to the issue at hand.

Original or very early papers that talk about using cuttings to determine ecodormancy -- possibly showing that these terms and ideas evolved around the same time.

1. Of the original/early papers, which ones use cuttings? Most evidently here is Erez & Lavee (1971) and Lamb (1948);

From Erez & Lavee (1971), Excised shoots: Mature shoots 40-50 cm long, of the last season, were collected in the orchard.

And from Lamb (1948), In this study a large number of canes were cut October 14 and stored with their butts in water at 37.4 degrees F and 26.6 degrees F.

Now to see if they are using these cuttings to determine ecodormancy; quick refresher that **ecodormancy** refers to the state at which the dormant buds are able to burst and rely entirely on external factors, not internal ones like endogenous hormone ratios

Fig. 1. Effects of controlled temperature on breaking the rest of Latham raspberries. 1946.

The paper doesn't explicitly state ecodormancy as one of the things it's testing, but the figure does sort of reveal it; that at a certain time of accumulating sufficient hypothetical chilling, the time taken for budburst to

occur appears to flatline and does not decrease further, providing an implicit graphical depiction of ecodormancy

And to be honest, it seems like Erez & Lavee don't really bring up even the idea of ecodormancy much, so not worth using them as a reference for this.

2. Can we get ecodormancy from original/early papers through Web of Science instead? In Web of Science, the search term "ecodorman*" yields the year 1987 as [the first instance in the search list where a definition of the term is given](#) (although it's highly likely that, due to Web of Science not covering every single publication in the world, ecodormancy as an idea probably emerged a bit earlier; nevertheless, a good starting point). [The second oldest result gives Inoue \(1990\)](#), a paper on potted satsumas exposed to chilling conditions.

In the search term ((cutting* OR scion* OR excise*) AND (ecodorman*)) we get 20 results (though most don't seem that relevant, primarily experiments on adventitious rooting in winegrapes or molecular studies) [with the earliest being 1993](#) (which is Tamura *et al.*) and a total of 20 publications.

By the time Tamura *et al.* (1993) came out, ecodormancy was probably already an idea floating around, considering that the term is defined in that Web of Science search hit in 1987, but this was only 6 years prior so it's probably within reason to assume that people were thinking about this entire concept of cuttings/dormancy/budburst/chilling in general at this time period? And the first actual publication on an experiment was in 1990, just 3 years prior to Tamura *et al.*

Papers that discuss how well using % budburst and rapid leaf out at high temperatures for non-fruit trees actually works as a determinant of endo-dormancy.

Which of the papers currently in the refs list are not about fruit trees, or any agricultural-oriented species in general? Which papers talk about endodormancy explicitly? A lot of papers will touch upon how budburst is a sign of dormancy release, but I'm not sure if they discuss the validity of this approach...keep looking!

It would be easy to wonder if budburst and leaf out were valid determinants for **ecodormancy** considering these two are conspicuous phenological events, and it might fully be the case that demarcations of endodormancy are purely at the molecular scale. In order for an experiment to show that budburst and leaf out are good determinants of endodormancy, it would have to somehow eliminate the conditions that enable ecodormancy to exist at all; i.e. after dormancy induction is incurred, **ONLY** favourable conditions are supplied. I can't think of any paper that actually does this, so maybe the following are at least a little bit helpful.

1. This paper on Norway spruce talks about endodormancy release inferred from bud burst using grafts;

In all 3 years of the present study, BB% was in mid-October at or near zero indicating that all, or most, of the buds were in endodormancy at that time. BB% generally increased with accumulated chilling, indicating that endodormancy was released.

And it does check out that if no BB is occurring, endodormancy must not have been released yet. The researchers transported the grafted spruce into forcing conditions at different chilling durations, such that they achieved a plot of %BB with differing chill durations, which is essentially what a lot of other chill-duration-into-budburst-measurement papers did (but now it's not on a fruit tree). They also say this, which probably means something important;

Taken together, these findings suggest that no major change takes place in the environmental regulation of endodormancy release in Norway spruce when the trees get older. Rather, both small seedlings and 80-year-old trees appear to follow the traditional conceptual model of endodormancy release (Hänninen 2016, p. 94): chilling is the main driving force of endodormancy release, and the chilling requirement is met by mid-November (however, see also Basler and Körner 2012).

The only problem is that the authors don't assess the strength of the approach (using budbreak to gauge endodormancy release) considering that successful budbreak is the manifestation of endodormancy release, and endodormancy release is instead the critical date/time at which sufficient chilling has occurred. I suppose then the question becomes **“what percentage of budbreak needs to be attained such that we can confidently conclude endodormancy release has occurred satisfactorily?”**

2. Zhang *et al.* (2021) look to proving the existence of endodormancy in subtropical trees;

*When exposed to growth-promoting high-temperature forcing conditions, endodormant buds either do not burst at all or their bursting requires a longer time than is required after the chilling requirement of endodormancy release is met (Fuchigami *et al.*, 1982; Hänninen, 1990; Cooke *et al.*, 2012). On this basis, the existence of endodormancy and the chilling requirement in the different material categories was tested in three experiments, all sharing the same principle of a standard chilling-forcing design (Hänninen *et al.*, 2019).*

And they used bud burst, leaf out, etc. as their measurement scheme;

In the forcing conditions, the seedlings/twigs were inspected visually at intervals of two or three days to assess their phenological stage of development. In the seedlings of all four species, four developmental events of bud development were discerned: bud closed, bud swelling, leaf emergence, and leafout (Fig. S5). The timing of the last of the events, the leaf out, was recorded.

But did they talk about the validity of the assumption that endodormancy can be readily interpreted from bud break or leaf out? I mean technically it's true...if your temporal resolution is fine enough, I feel we can comfortably argue that these phenomena CAN indeed be good markers for endodormancy release, but is this I evaluated anywhere in their discussion? Sadly, no. And to be honest I have not yet found a paper that bluntly talks about this, because it seems like it's a deep-rooted assumption that starts with Fuchigami *et al.* (1982), their contemporaries, and their predecessors.

3. Zhang *et al.* (2023) might offer some insight into this historical problem of not knowing when endodormancy release occurs (though now with so much molecular research, we do know more about what genes are upregulated in expression, physiological features, etc.);

Nevertheless, whichever definition of the Δt is used, the classical approach described above is essentially a black-box one, for it makes use of no observations or measurements of the growth-arresting physiological and molecular conditions or their removal inside the buds per se. In other words, the invisible endodormancy release that has taken place in the buds under the chilling conditions by the time of the transfer to the forcing conditions is determined on the basis of the implications of the endodormancy release for the occurrence and timing of the visible bud burst in the forcing conditions.

Here they directly address the fact that chilling time or other kinds of models that use chilling duration/temperature/etc. as input and days to budbreak as the output are essentially lumping endo- and ecodormancy together, since there's no molecular scale work done to show when the former ends and the latter begins. They also bring up an interesting point here, though it fits more into the first bullet point in the issue than this one;

However, though the experimental technique for determining the chilling response of endodormancy release is straightforward, it is laborious and time-consuming. This is evidently the reason why the chilling response of endodormancy has usually not been determined experimentally. Rather, the response has mostly been determined either a priori, or by means of inverse modelling, meaning that the values of all model parameters (not only the ones related to chilling effects) are estimated by fitting the model statistically to observational long-term phenological and air temperature records.

Which made me think of the first point in the issue, with the whole recursive data to model to data to model problem going on. In a similar vein, Jewaria *et al.* (2021) gives an example of this problem of “inverse modelling”;

*It should be noted, however, that the model development by Chen *et al.* (2017) was based on the technique of inverse modelling, an approach in which process-based models are fitted to observational long-term phenological records. It has been known since the pioneering study by Hunter & Lechowicz (1992) that this method involves an exceptionally high degree of uncertainty and that biologically unrealistic models are quite often obtained with it (for a recent discussion, see Hänninen *et al.*, 2019).*

Every time I look for papers that review endodormancy release and leaf out timing it's always about fruit trees, whether it's almonds or cherries or peaches or kiwi etc. BUT also, like Zhang *et al.* (2023), Fuchigami *et al.* (1982) reiterates from Sarvas (1973; 1974) that;

Attempts to relate growth stages to environmental factors have had limited precision because, to quote Sarvas, “there are no suitable, easily observable phases that can be accurately measured”.

Which is presumably why Fuchigami *et al.* (1982) then proceed to spend the entire paper defining certain growth stages in a quantitative way.

4. Do any of the molecular papers on hybrid poplar talk about the difference between endo- and ecodormancy at all? These papers might both lean into the black-box problem as mentioned above, but the problem with that

approach was that external inputs were reflected by external outputs; that is, the boundary between endo- and ecodormancy couldn't be seen, because **endodormancy** is internal. But these poplar papers are now utilizing internal mechanisms like molecular genetics and gauging the external response, which is the break of ecodormancy. While the papers on bud induction and shoot elongation genes in poplars didn't yield any major clues, [this paper on the herbaceous peony](#) talks about cytological and molecular signals for endodormancy release, echoing [this paper on glucanases](#) opening vasculature for the same purpose in the tree peony.

[This next paper is unfortunately about apricots](#), but suggests the initiation of male meiosis as another marker for endodormancy release.

What to do next? Maybe look through the citations for zhang2023 and jewaria2021 more deeply...

| *Examples where researchers developed falsifiable predictions from models of chilling*

This one I may not be able to answer confidently, in full honesty, but I can certainly try!