

Seed Germination

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Fifteen years ago I began a study of seed germination. At present over four thousand species have been studied. These studies differ from all previous work in that variables are precisely controlled, rate curves are emphasized rather than just percent germination, and the rate curves are analyzed by chemical rate theory. The results dramatically revise concepts in the field and pave the way for highly efficient methods of propagating plants from seeds. The following examples illustrate some of the highlights of the work.

Gibberellins have a powerful effect on the course of germination for many species, and they can be an absolute requirement for germination. Many cacti such as *Echinocereus pectinatus* are tiny plants growing in harsh environments. To survive the blazing sun and infrequent rains the seeds must germinate in shade in a pocket of deep leaf mold. The seeds have evolved a clever method for detecting such a place. This is to require for germination a specific chemical, a gibberellin, which is produced by action of the fungi on the leaf mold. Seedlings were obtained by treating the seeds under moist conditions at 70F with gibberellic acid (GA_3). In samples of over 2000 seeds not a single germination occurred in any other treatment. The germination follows a first order rate equation precisely out to over eight half lives which is a precision rarely seen even with small molecules in a chemical laboratory. The induction period was six days and the half life was 4.9 days. The GA_3 treatment is absolutely essential for the growing of this species from seed.

Over two hundred species of cacti have been studied and about half were found to require GA_3 for germination. Other species with this germination requirement are the rosulate violas from the Andes, *Ranunculus lyalli* from Mount Cook in New Zealand, and a number of plants from the cold deserts of Nevada and Eastern Oregon and Washington such as *Romneya coulteri*, *Ribes cereum*, and *Dendromecon*.

The gibberellin requirement is also found in a few species from the woodlands of Eastern North America such as *Sambucus pubens* and *Cornus canadensis*. The shrub *Alangium platanifolium* also has this requirement. There is clear evidence that *Caulophyllum thalictroides* and *Sanguinaria canadensis* require gibberellins other than GA_3 so that this field is complex and needs much more study.

In order to control variables such as the gibberellin factor, all experiments were conducted in sterile high-wet-strength paper towels and polyethylene bags. The techniques were highly efficient, and five hundred experiments can be conducted in a space of 1 ft³.

An interesting group are species that require oscillating temperatures for germination. Daily oscillations between 40 and 70F are typically effective. Obviously such a pattern is designed to cause the seeds to germinate in spring or fall. Examples are *Trollius laxus* and *Cornus florida*. Such seeds can be germinated by placing the seeds outdoors in moist media, but the oscillating temperatures can be duplicated in the laboratory. A set of experiments were conducted on *Cleome serrulata* in which the periods at 40F and 70F were varied over wide ranges. As

might be expected daily oscillations (12 h) were about optimum. This pattern is in accord with chemical rate theory.

In many species specific time-temperature cycles are needed to effect germination as in *Eranthis hyemalis*. The seeds must be kept moist at 70F for three months to complete the destruction of the first blocking mechanism and then shifted to 40F where a second blocking mechanism is destroyed. After exactly 55 days at 40F an extremely rapid germination suddenly commences. This follows an exact zero order rate plot with a rate of 25% per day so that germination is complete in four days. The period at 70F and the 55 days at 40F are periods of maximum metabolic activity in terms of the chemical reactions destroying blocking mechanisms. Terms such as "breaking dormancy" or "double dormancy" are hopeless misconceptions and must be immediately abandoned.

Many species germinate at 40F and will not germinate at 70F. This is typical of plants from cold desert areas where they must get off to a fast start in spring as soon as the ground thaws in order to escape the desiccation of summer. *Rhodophiala montanum* from the Andes is a good example. Incidentally I am hybridizing these rhodophialas as they have the potential to become hardy garden amaryllis.

Many species have induction periods as for example *Abeliophyllum distichum*. After 25 days moist at 70F germination begins and follows a zero order rate law with a rate of 7% per day. The 25 day induction period is a time when a blocking mechanism is being destroyed and not a period of dormancy.

Light has long been known to initiate germination in certain species, but it has not been appreciated that the effect of light is to destroy blocking mechanisms and that the behaviors can be complicated. Fresh seed of *Buddleja davidii* requires light to germinate, but this requirement dies off with time so that after 2 years of dry storage, the seeds germinate about equally in light or dark. The common watermelon (*Citrullus lanatus* syn. *C. vulgaris*) and others cucurbits show this pattern. *Weigela florida* is typical of many species whose seeds germinate either in light or in dark with GA₃. The effect of light can be combined with other patterns as with *Primula kisoana*. This seed will germinate only if dry stored for 6 months followed by moist condition with light. Incidentally, this is one of the best primroses for gardens in eastern U.S. and should become a great favorite now that its germination pattern is known.

Some species, such as *Halesia tetraptera* (syn. *H. carolina*), have not germinated until after 1 to 4 years of temperatures alternating between 3 months at 70F and 3 months at 40F. Perhaps a way will be found to increase the germination rate, but for the moment the most efficient method of handling such seeds is to keep them in moist paper towels in polyethylene bags for the long period until germination starts. This much reduces the cost of labor and capital investment.

The above patterns all involve a chemical mechanism for blocking germination and about 95% of the 4000 species studied use chemical methods. The remaining 5% use a physical method for blocking germination and this is almost always an impervious seed coat. An example is *Laburnum vossi* which germinates within a few days if the seed coat is punctured and the seeds placed in moisture at 70F. The old terminology of calling this "scarification" is misleading because scratching the surface is not effective. A particularly troublesome and misunderstood group are the asiatic maples. These have a tough hard outer seed coat and a thin pliable inner seed coat. However, it is the inner seed coat that is impervious. I have done

considerable experimentation to develop an efficient method of removing the tough outer seed coat.

Every aspect of seed germination involves chemical processes that have precise and reproducible rate plots. This includes the dying of seeds in dry storage and the dying of seeds in moist conditions unsuitable for germination. There is no substitute for knowing all of these rates precisely. Only then can one organize the production of plants from seeds with the maximum efficiency in the use of labor and capital investment.

The mid morning session on Tuesday was moderated by Scott Clark.