

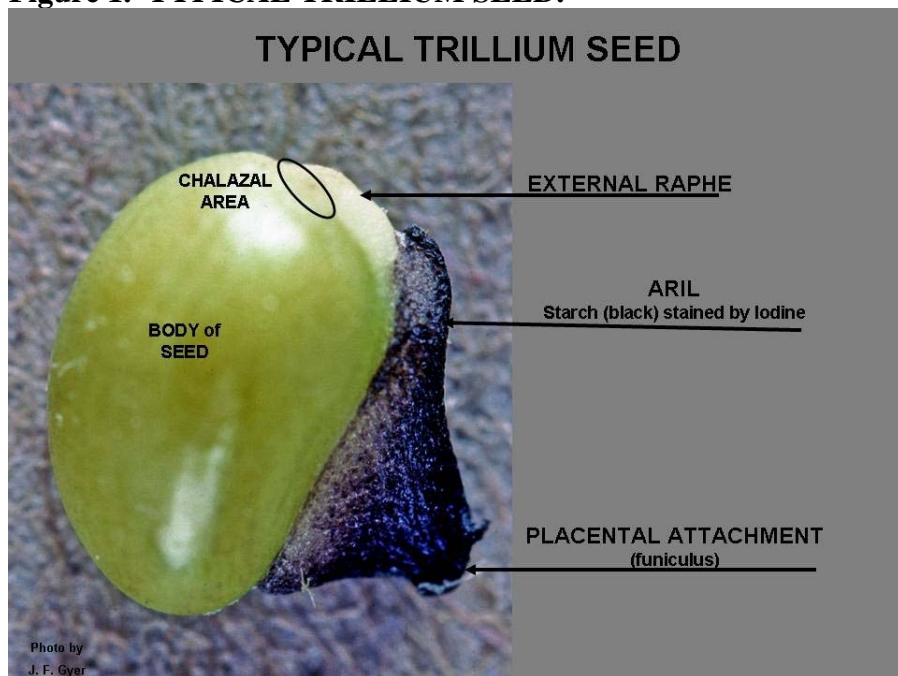
## THE DARK SIDE OF TRILLIUM

by  
John F. Gyer

When I started to grow trillium from seed, Dr. Norman Deno was just beginning his extensive study of seed germination. His germination technique was straightforward. Seeds were put on moist paper towels, stored in plastic bags, and cycled from warm to cold temperatures. I thought this would be ideal for trillium germination because it offered the chance to shave a year off the usual 7-year progression from seed to flowering plant and it gave me a chance to see the process of germination. In the end I did not find it a reliable way to speed the germination process, but I did see some remarkable things that I want to share with you.

Most of my early germination observations were done with *Trillium grandiflorum* seed that Winterthur allowed my late wife, Janet, and me to collect from the large naturalized population in Azalea Woods. The seeds (Figure 1, TYPICAL TRILLIUM SEED) are waxy, roughly egg shaped, and have an attached aril. The aril is the organ that trillium use to disburse seeds in their environment. Some ant species and hornets are attracted to volatile compounds that come from the aril directly or from the fermentation of the outer layer of starch filled cells. These insects carry trillium seed to new places in the woods as they feed on the aril. When they finish, the seed is discarded for their mandibles cannot penetrate its waxy surface. I have heard that fire ants are an exception. They have stronger "jaws". They can eat into the seed and destroy it. Normally, though, the discarded seed lies on the forest floor and, with luck, the germination process begins.

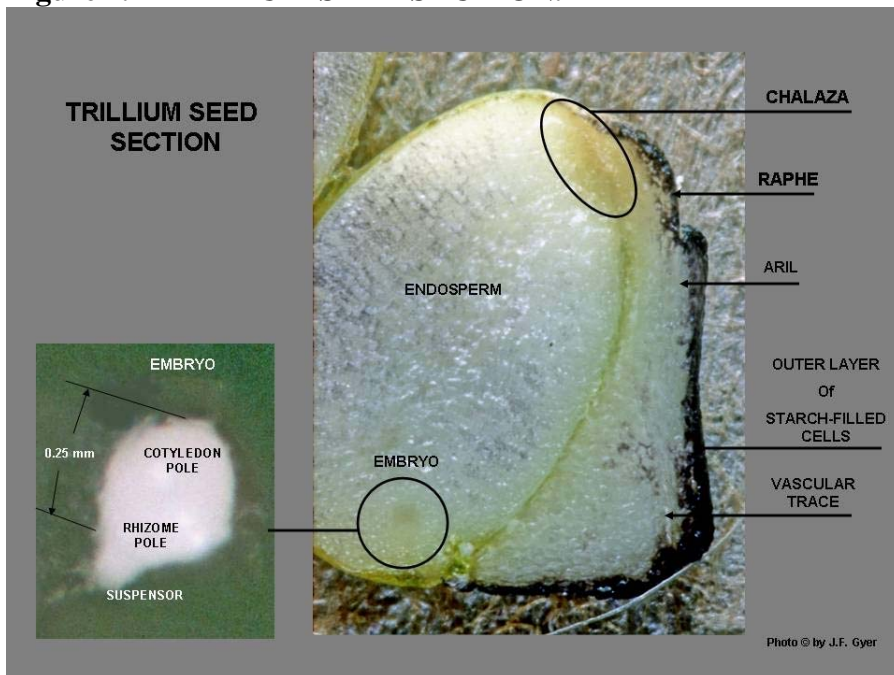
**Figure 1. TYPICAL TRILLIUM SEED.**



I was curious about this process. What went on during germination? Why did it take about 18 months for the cotyledon to appear above ground? The literature named the process "double dormancy" but just naming it seemed inadequate and incomplete. I wanted to find out what was going on INSIDE the seed.

When I cut the seed open (Figure 2, TRILLIUM SEED SECTION) I found a large volume of endosperm and an embryo so small that I had to slice at least 100 seeds before I learned where it is located. The embryo is roughly a sphere about 0.25 mm in diameter. In *T. grandiflorum* the endosperm is about 800 times the embryo volume. The endosperm is essentially stored sunlight. Photosynthesis in the leaves captures the sun's energy and the plant stores some of it in the endosperm as food that the embryo uses during its growth into a seedling.

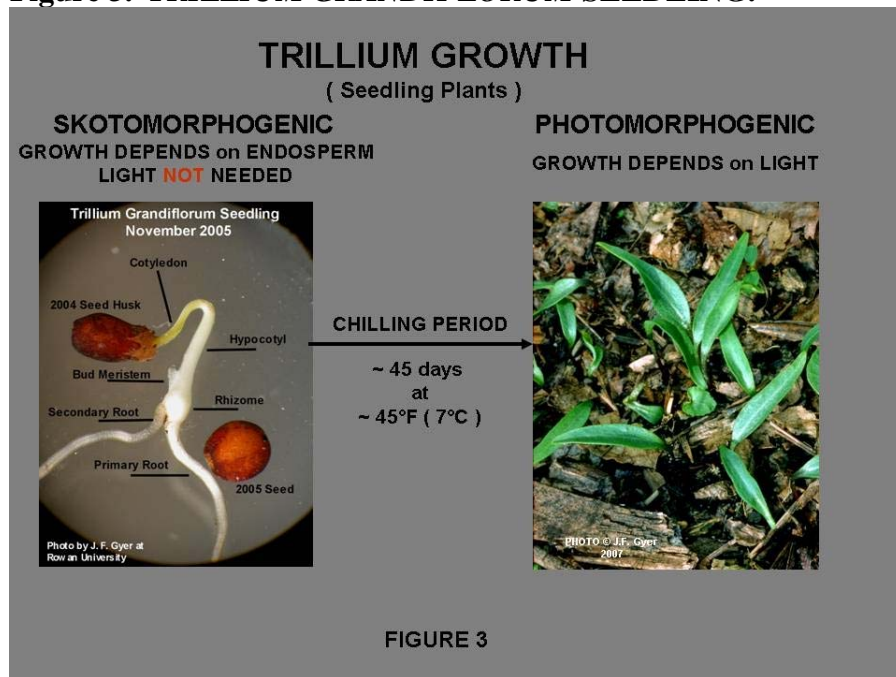
**Figure 2. TRILLIUM SEED SECTION.**



The embryo may be active or dormant when the seed is harvested. For *T. grandiflorum* seed age, measured as days between pollination and harvest, determines the depth of embryo dormancy. The embryos of older seeds are more likely dormant than are those of younger seeds. A cold rest period changes a dormant embryo into an active one.

Once active, the embryo begins to digest the endosperm and absorbs the nutrient it needs through its growing cotyledon. In about 60 days at moderate temperatures (65°F to 75°F) the young rhizome emerges from the seed husk. Although unseen by most gardeners because the seed is underground, rhizome emergence signals trillium seed germination. For the next 60 or so days the trillium seedling grows underground into a fully independent plant. This underground seedling growth is entirely supported by the endosperm, the sunlight energy captured by photosynthesis the previous spring and stored in the seed for the seedling's use. The seedling is a fully independent plant and needs only chilling to change its hormonal balance so that its cotyledon can elongate in the warming soil of spring and begin photosynthesis. (Figure 3, TRILLIUM GRANDIFLORUM SEEDLING)

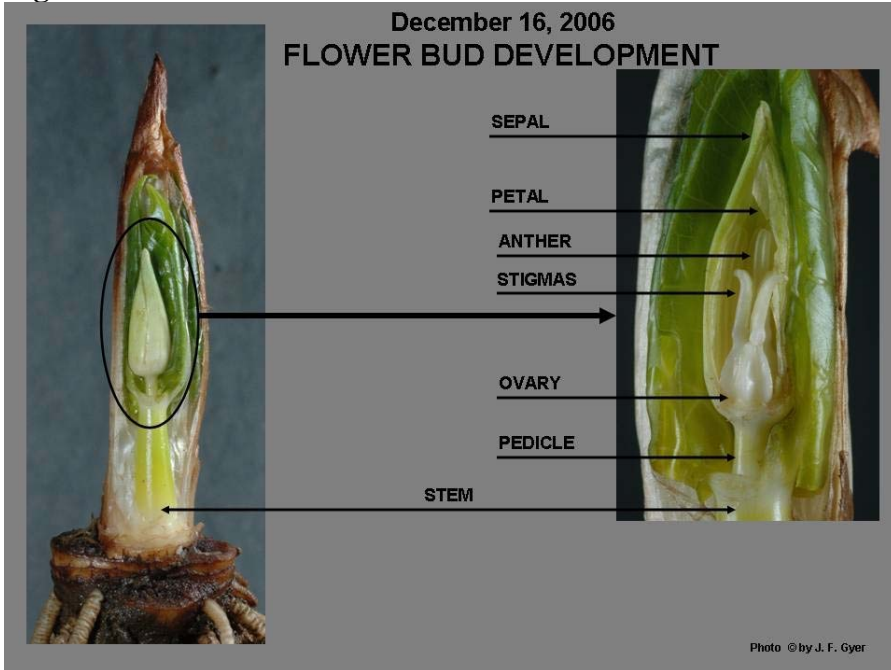
**Figure 3. TRILLIUM GRANDIFLORUM SEEDLING.**



I was intrigued that seedling growth happens underground. This growth does not require any direct sunlight. I looked in botanic literature to see if there was a term that could name this process. I found none that fit, but some ecologists have used the term "skotomorphic" to describe the elongated growth seen in many plants when they are crowded or deprived of light. I adopted their term and use it to describe the active underground phase of trillium seedling growth. I call it the skotomorphogenic growth phase. The growth phase that supports photosynthesis is the photomorphogenic phase.

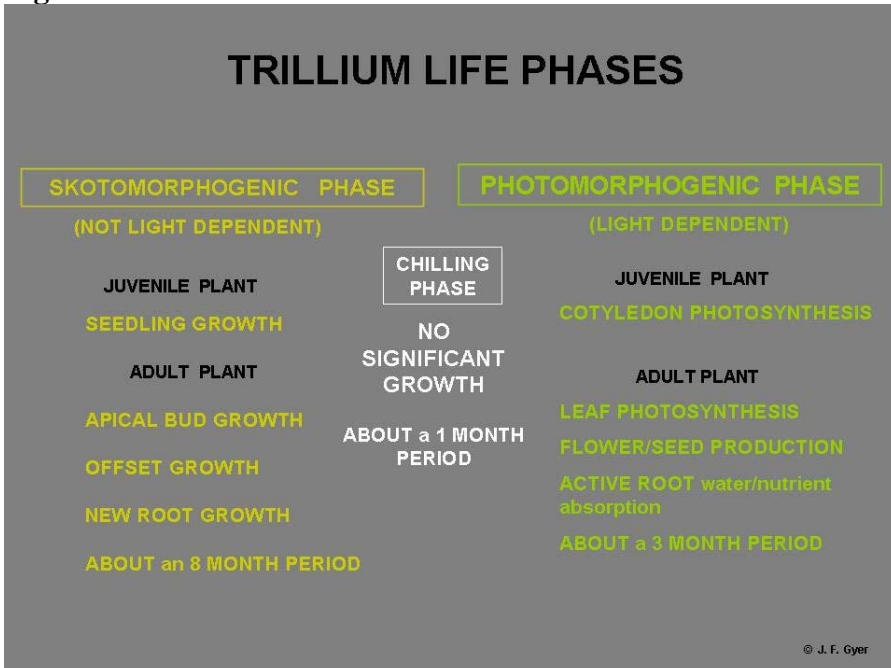
I was still puzzled and asked myself; "If the seedling shows skotomorphogenic growth, does the adult trillium do the same?" Pennsylvania Power and Light had given me permission to monitor the relation between environment and trillium growth at their Shenk's Ferry wildflower preserve. During that monitoring I found that adult trillium rhizomes have skotomorphic growth in both their apical buds and their roots at the same temperature and soil moisture conditions as those that induce seed germination and seedling growth. New roots form just below the apical bud about the time the flowers began to fade. By early July both new roots and the apical bud are in active growth. By mid-December the flower buds are fully formed, the leaves are green and ready for their spring expansion. (Figure 4, FLOWER BUD DEVELOPMENT)

**Figure 4. FLOWER BUD DEVELOPMENT.**



Trillium alternates between an underground skotomorphogenic growth phase in the summer and an above ground photomorphogenic phase in the spring. This alternation between growth phases begins when the plant starts life as an active embryo and ends when it succumbs to environmental insults sometimes 40 or more years later. Although there may be no leaves present, trillium is not dormant during the summer. It is growing underground and preparing for the next spring. Trillium become briefly dormant only when winter temperature drops low enough to halt active skotomorphogenic growth. (Figure 5, TRILLIUM LIFE PHASES)

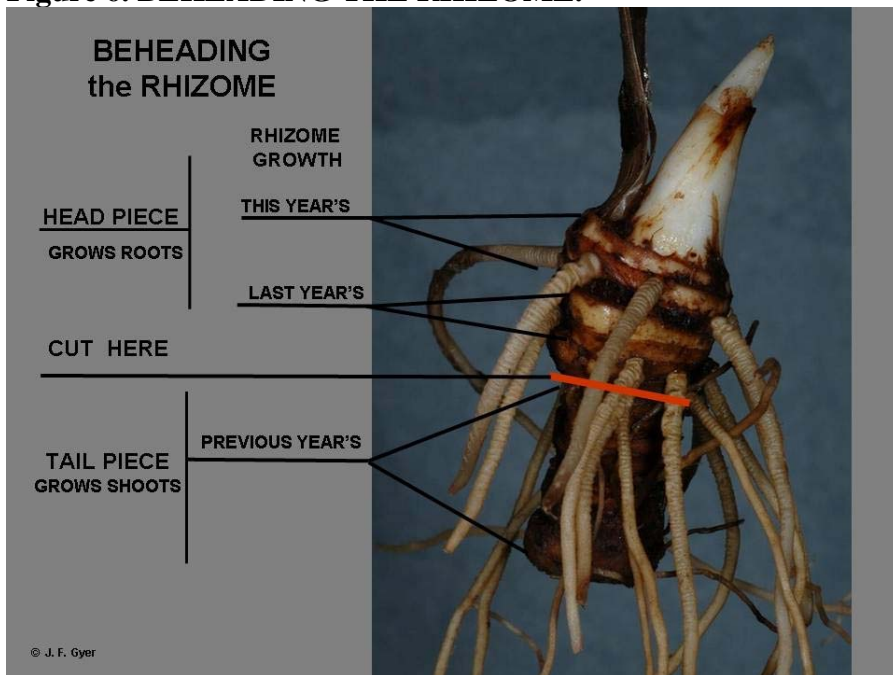
**Figure 5. TRILLIUM LIFE PHASES.**



The best time to transplant trillium or to induce offset production by a process called "beheading" turned out to be just as the flowers fade - the start of skotomorphogenic growth. This is the time when new roots are beginning to form and after early photosynthesis has added fresh reserves to the rhizome.

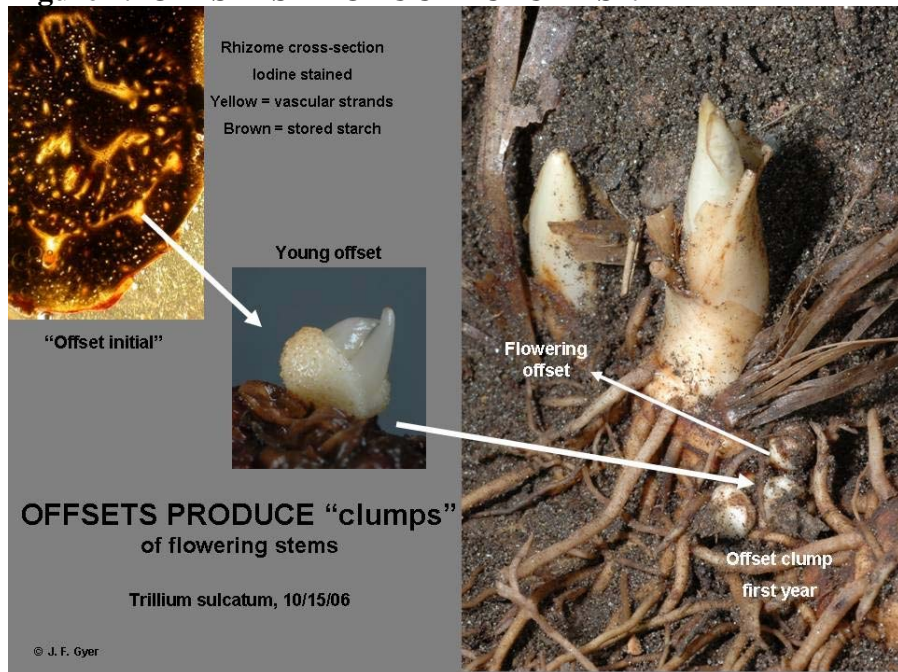
Beheading is a way of creating clones of a plant that you particularly like. It involves cutting the rhizome just below active root growth that happens only in the most recent 2 to 3 years of rhizome growth. (Figure 6, BEHEADING THE RHIZOME) When the upper part of the rhizome with the bud and new roots is planted, growth will continue as if nothing had happened. In the older part of the rhizome there are internal cambium-like cells, the plant version of stem cells, which react to the changed hormone environment by beginning active growth. These cells grow while the soil is warm during late spring, summer and fall. They push out from the rhizome and establish small offshoots that behave just like seedlings. They will produce leaves after the chill of their first winter and slowly grow into independent plants identical to the parent.

**Figure 6. BEHEADING THE RHIZOME.**



Offsets form spontaneously in some species. (Figure 7, OFFSETS PRODUCE "CLUMPS") In other species some individuals form them more abundantly than others. Those individuals that form offsets can produce lovely large clumps of stems.

**Figure 7. OFFSETS PRODUCE “CLUMPS”.**



The clumps that arise from rhizome offsets are different from the 2 or 3 stems that may come from the rhizome apex of particularly strong plants. Multiple apical stems begin life at the start of skotomorphogenic growth. (Figure 8, 2006 APICAL BUD, TWO-STEMMED RHIZOME) They arise because more than one stem bud is activated in the rhizome apex. Trillium likes to look ahead and within the apical bud there maybe stem buds enough for the next 3 years of growth. A strong root system on a large rhizome can activate one or more of the reserve buds in addition to the bud destined to produce flowers the next spring.

**Figure 8. 2006 APICAL BUD, TWO-STEMMED RHIZOME.**

