induction and release. Seeley focuses attention on the endodormancy of woody species and stresses the point that in the absence of direct methods, indirect methods must be used to quantify seed dormancy. The immensity of the problem is clearly evident in the remark by Seeley “...in the obvious unknown ED (endodormancy) milieu, how can we measure its intensity, its transition and its release?” Fuchigami and Wisniewski emphasize the benefits of developing quantitative systems of classifying dormancy in buds. They present a conceptual numerical model based on growth stages divisible into numerical units that would likely lead to improved understanding and quantification of dormancy. Faust et al. discuss the roles of hormonal, chemical, and physical factors in bud dormancy, making a compelling argument for the role of bound vs. free water in the control of endodormancy. This article proposes several biochemical and physiological approaches for measuring dormancy.

The workshop was the first attempt at quantifying plant dormancy. It provided an excellent opportunity to review the state of our knowledge of plant dormancy, the differences and similarities in seed and bud dormancy, and the various approaches used to quantify them. The participants hope that it will serve as a forerunner for future workshops or colloquia for reporting progress in this important area of plant development.

Quantification of Seed Dormancy: Physiological and Molecular Considerations

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Physiological and biochemical controls needed to induce, maintain, and release seed dormancy are not clearly understood and hence it has been difficult to quantify dormancy. The studies on dormancy have dealt with the changes in embryo growth potential or germinability in relation to the controlling factors within the embryo, covering structures and environmental stimuli or their combinations in a dose-related fashion. More recently, attempts have been made to relate dormancy maintenance and release to temporal cellular and molecular changes, and conflicting theories or mechanisms for the control of dormancy have been advanced. This situation has made the task of quantifying dormancy quite difficult. For example, several genes or cDNA clones have been identified from dormant seeds and the temporal changes in the mRNA transcript levels of these genes during hydration, using labeled cDNA as a probe, have been studied. The transcript levels increase (Toyomasu et al., 1995) or decline and disappear (Goldmark et al., 1992; Li and Foley, 1995) in response to GA.

This article describes the various approaches that have been employed to quantify dormancy induction, maintenance, and release. They are based on the performance of seed in relation to the changes in the strength of the embryo covering structures, the effects of the environmental stimuli, responsiveness to hormones, hormone concentrations, RNA and protein synthesis, mRNA transcript levels of a cDNA clone, or combinations thereof.

COVERING STRUCTURES AND EMBRYO GROWTH POTENTIAL

Strength of covering structures and dormancy intensity. Indian ricesgrass [Oryzopsis hymenoides (Roem. & Shult.) Rick] seeds have seedcoat (lemma and palea) and embryo dormancy (McDonald and Khan, 1977). Increasing the period of scarification with sulfuric acid progressively increased the germination percentage. Germination percentage increased linearly with the increase in scarification time (Fig. 1). Younger seeds (1971 vs. 1970 harvest) were more resistant to

INDIAN RICE GRASS

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Fig. 1. Relationship between sulfuric acid scarification time and germination of Indian ricesgrass seeds harvested in 1970, 1971, and 1973. Appropriate regression equations were generated to fit the data (from McDonald and Khan, 1977).
the scarification treatment, required longer period for optimum scarification (a period beyond which seeds were adversely affected by scarification), and had lower peak germination percentage compared to the 1970 seeds. Although the linearity of the response extended over a longer period in the younger seeds, their peak germination percentage was lower than that of the older seeds, indicating that they were not only more resistant to scarification but also generated a lower embryo growth potential. The curves show that, beyond a certain time, scarification adversely affects germination, presumably as a result of acid injury to the embryo. These studies indicate that changes in embryo growth potential and seed coat strength occur during storage and both of these changes can be used to quantify dormancy.

**Growth potential changes by high temperature shift and dormancy intensity.** Intact or sulfuric acid scarified curly dock (Rumex crispus L.) seeds fail to germinate in darkness at 20, 25, or 30 °C. A 1-h temperature shift to 40 °C, applied at various times to scarified seeds during a dark soak at 25 °C, progressively increased the effectiveness of the shift to promote germination (Hemmat et al., 1985). Shifting at 24 h caused nearly 100% germination. The shift applied after 48- or 72-h imbibition was less effective, leading to only 75% and 45% germination, respectively (see below for reduced embryo growth potential during prolonged dark soak). A similar germination response pattern was found upon application of the 1-h-40 °C shift to intact (non-scarified) seeds soaked in darkness, but the peak germination after the 24-h soak reached only 15%. These data show that the high temperature shift permits the detection of temporal changes in the dormancy intensity or embryo growth potential during the dark soaking and is facilitated by scarification. The high-temperature shift influences a membrane-associated event that evidently is related to processes affecting embryo growth potential.

**ENVIRONMENTAL STIMULI**

**Period of dark soak and dormancy intensity.** Seeds of several species requiring light for germination are rendered progressively more dormant with increase in the dark soak time, while light or GA applied during soaking prevents dormancy induction. Seeds of ‘Grand Rapids’ lettuce (Lactuca sativa L.) germinate poorly or not at all at 25 °C. When the seeds are depedicaped at 6 h of dark soaking, all germinate in darkness, indicating that the removal of the pericarp lowers the restraint by the covering structures to below that of the germination or growth potential needed for radicle protrusion (Khan and Samimy, 1982). However, if the seeds are depedicaped after longer periods of dark soaking, a dormancy is progressively induced and after a 24-h soak even the depedicaped seeds fail to germinate. Thus, the degree of dormancy induced, as evidenced by decreased growth potential, can be quantified in light-requiring seeds, based on the duration of the dark soak and the nature of the seed coat restraint. As the restraining forces of the pericarp and endosperm on the embryo are measurable (Tao and Khan, 1975), the forces needed to prevent germination are measurable. Dark dormancy (skotodormancy) can also be released by irradiation or moist-chilling. Perennial goosefoot (Chenopodium bonus-henricus L.) seeds, for example, were made completely germinable in darkness by moist-chilling at 5 °C for 1 month. A dark soak of prechilled seeds in –0.86 MPa polyethylene glycol-6000 (PEG) solution gradually induced a dormancy and by 21 days of soaking, the seeds were rendered completely dormant (Fig. 2) (Khan and Karssen, 1980). Dormancy induction was prevented (and the rate of germination enhanced) in seeds treated with light or GA (data not shown) during the osmotic soak. Thus, a period of dark soak in an osmotic solution can be used to quantify the degree of dormancy induced in a seed with moist-chilling and light requirement.

**Temporal relationship between P_a action and dormancy intensity.** The time needed for the P_a (active form of the phytochrome) to fully act to release the dark dormancy in ‘Grand Rapids’ lettuce seeds is ~8 h at 25 °C and is referred to as the ‘escape time’ from inhibition by far-red irradiation (Borthwick et al., 1954; Ikuma and Thimmann, 1960). If the far-red irradiation is applied immediately after red irradiation, dormancy is not released. A progressively greater release of dormancy occurs if the period between the application of red and far-red irradiation gradually is increased to 8 h, when the dormancy release is complete. After P_a has acted fully to release the dormancy, its reversion to P_f (inactive form of the phytochrome) by far-red is of little consequence. Thus, the time of P_a action is a good measure of the extent of dormancy released and varies greatly among photosensitive seeds (Toole et al., 1973).

**Temporal relationship between moist-chilling period and dormancy intensity.** Moist-chilling or stratification at 1 to 10 °C releases dormancy in a wide variety of seeds (Stokes, 1969). An excellent relationship was obtained between the length of chilling period and growth in pear (Pyrus communis L.) embryos excised following moist-

![Image](https://example.com/image)

**Fig. 2.** Effect of various durations of (A) light and (B) dark soaking of moist-chilled Chenopodium bonus-henricus seeds in –0.86 MPa PEG solution on (A) dormancy prevention and (B) dormancy induction, expressed as percent germination. Following the osmotic soak seeds were washed and germinated in water in darkness at 12/22 °C (from Khan and Karssen, 1980).

![Image](https://example.com/image)

**Fig. 3.** Relationship between the period of moist-chilling of pear seeds and the growth, expressed as weight, of excised embryo (from Khan and Heit, 1969).