

# Cucurbit Seed Development and Production

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ADDITIONAL INDEX WORDS. **seed vigor, germination, seed aging, fruit development**

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**SUMMARY.** Seed production in the family Cucurbitaceae is more complicated than in dry-seeded grain crops because seeds mature within a moist fruit and are often held at high moisture content for several weeks before seed harvest. Muskmelon (*Cucumis melo* L.), a member of this family, was used as a model system to contrast seed development with crops that are dry at maturity. A detailed time course for 'Top Mark' fruit and seed development is presented based on previous studies. In muskmelon fruit, precocious germination is inhibited osmotically by the low water potential of the surrounding fruit tissue. Muskmelon seeds exhibit primary dormancy that affects viability very early in development but has a greater effect on seed vigor and is removed by afterripening during dry storage. Osmotically distended or fish-mouth seeds are dead seeds that occur in cucurbit seed lots after aging kills the embryo without disrupting the semipermeable endosperm that completely surrounds and protects the embryo. Cucurbit seed crops should be harvested before the onset of fruit senescence to prevent aging of the seeds inside. Open-pollinated cucurbit seed crops are frequently once-over mechanically harvested. Mechanical harvesting combines seeds from many stages of development into a single seed lot, which may adversely affect quality and increase seed to seed variability. Hand harvesting cucurbit fruit at the optimal stage of development could improve seed quality in some instances but is more costly and time consuming and would increase production costs.

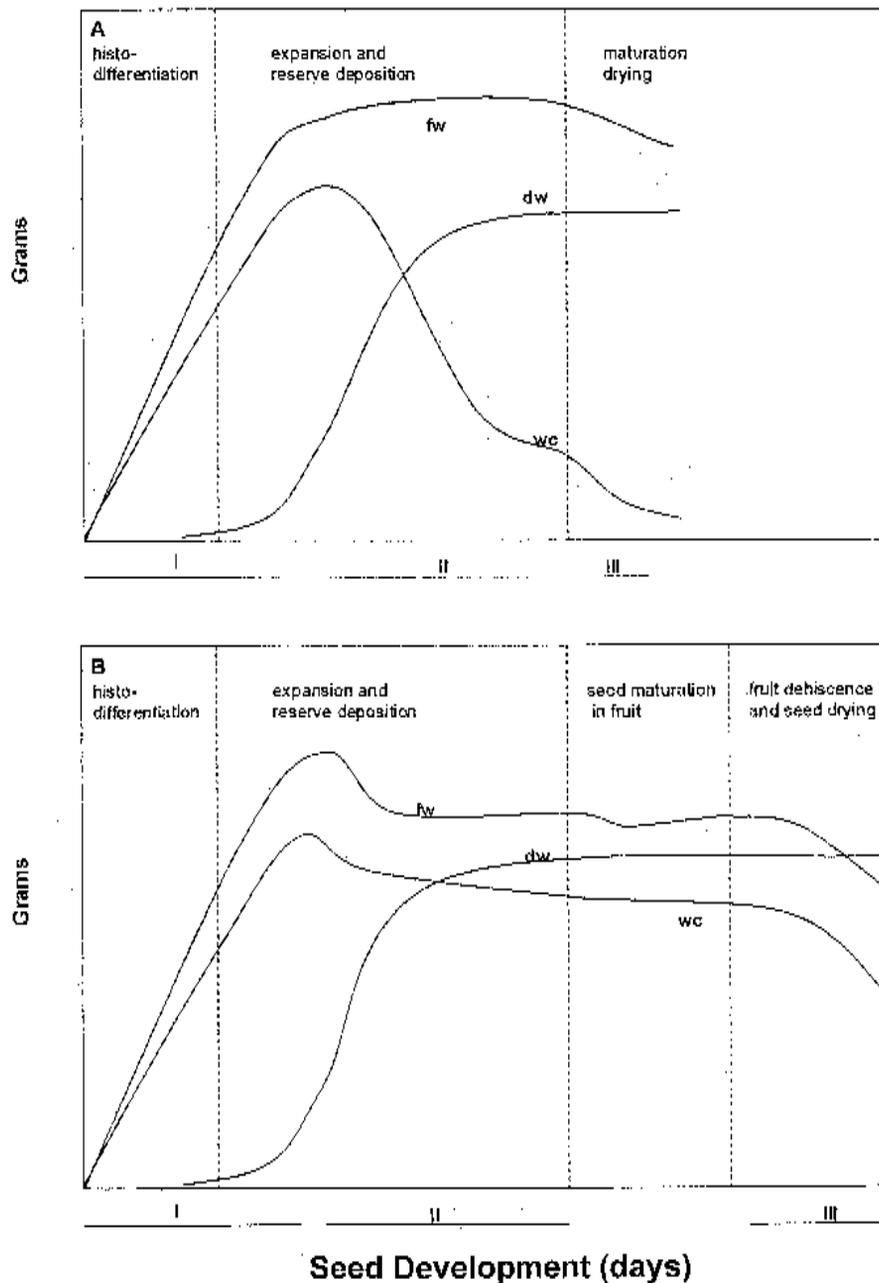
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Seed maturity in dry-seeded grain crops such as wheat (*Triticum aestivum* L.) and soybean [*Glycine max* (L.) Merr.] is punctuated by desiccation (Fig. 1A) (Ackerson, 1984; Barlow et al., 1980). In many crop species, water movement between the maternal plant and fruit is broken at seed maturity, allowing desiccation of the fruit and seed to occur while the plant remains fully hydrated (Adams and Rinne, 1980; Barlow et al., 1980). In species that produce seeds inside a fleshy fruit, such as tomato (*Lycopersicon esculentum* Mill.), seeds mature and remain within a relatively moist environment where desiccation is prevented or delayed until after fruit senescence (Fig. 1B). Seed development in fleshy-fruited species has received less research attention than in dry-seeded grain crops. We have investigated seed development in crops that maintain high seed moisture contents to determine the effect on seed quality.

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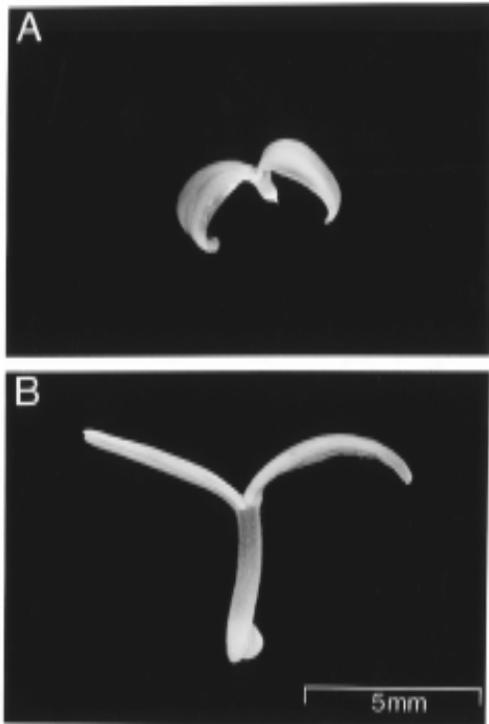


**Fig. 1. A relative comparison of seed fresh weight (fw), dry weight (dw), and water content (wc) changes during development for dry-seeded grain crops whose development is punctuated by dryness (A), and crops that develop in flesh fruit like most members of the family Cucurbitaceae (B). Three major phases in seed development are compared: I, rapid gain in fresh weight because of cell division and early expansion, II, rapid dry weight accumulation driven by cell enlargement, III, loss of fresh weight during drying. Figures contrast relative differences in seed weight for developing wet- and dry-seeded crops based on previous reports in the literature; 28.4 g = 1 oz.**

Cucurbit (from the family Cucurbitaceae) seeds remain hydrated inside developing fruit well after maximum dry weight accumulation is obtained (Welbaum and Bradford, 1988). This raises interesting questions about how precocious germination is prevented and when seed harvest should occur for best quality. Muskmelon provides a good model system for the study of seed development in fleshy-fruited horticultural crops because its seeds remain near full hydration for weeks after the accumulation of maximum seed dry weight and edible fruit maturity (Fig. 1B) (Welbaum and Bradford, 1988). Cucurbit seeds grown for propagation have significant economic value in the U.S., and California is the leading producer. In a recent year, California alone produced almost 7,285 ha (18,000 acres) of cucurbit seeds valued in excess of \$25 million (University of California, 1992). In this paper, I will review cucurbit seed development with special emphasis on muskmelon seed and fruit.

Muskmelon embryos develop the ability to germinate sequentially well before the accumulation of maximum dry weight which occurs roughly 35 d after anthesis (DAA) for the cultivar Top Mark. Initially, developing seeds cannot germinate if removed from the fruit and incubated on water. However, as early as 15 DAA, some embryo tissue growth is observed if testa and endosperm tissues are removed and isolated embryos are placed in the presence of water (Fig. 2A). For example, from 15 to 18 DAA, the cotyledons of isolated immature muskmelon embryos expanded and produced chlorophyll when incubated on blotter paper saturated with water at 25 °C (77 °F). No other embryo tissues grew when incubated under similar conditions at this stage of development (Fig. 2A).

At ≈20 DAA, hypocotyls elongated and cotyledons expanded, but root and shoot meristems were not competent to grow when isolated embryos were incubated under favorable conditions (Fig. 2B). At 25 to 30 DAA, roughly 40% of epicotyls and roots from isolated embryos grew, while the remaining 60% showed only cotyledon and hypocotyl expansion (Welbaum and Bradford, 1989). By 35 DAA, the time of mass maturity (maximum dry weight accumulation), all embryonic tissues grew and normal seedlings developed but only when the testa and endosperm were removed. The germination percentage of intact seeds was <50% at mass maturity (Fig. 3). Greater than 95% viability was not obtained by newly



**Fig. 2. The growth and development of immature 'Top Mark' muskmelon embryos after isolation from the seed and incubation in water for two weeks at 25 °C (77 °F). (A) At 15 DAA, cotyledons were the only embryo tissue capable of growth. Growth occurred when the seed coats and endosperm envelope were removed and the embryos were incubated in water (scale identical to that in panel B). (B) At 20 DAA, in addition to cotyledon growth, hypocotyl growth was also possible in isolated embryos, although the embryonic axis was not yet capable of growth; 25.4 mm = 1 inch.**

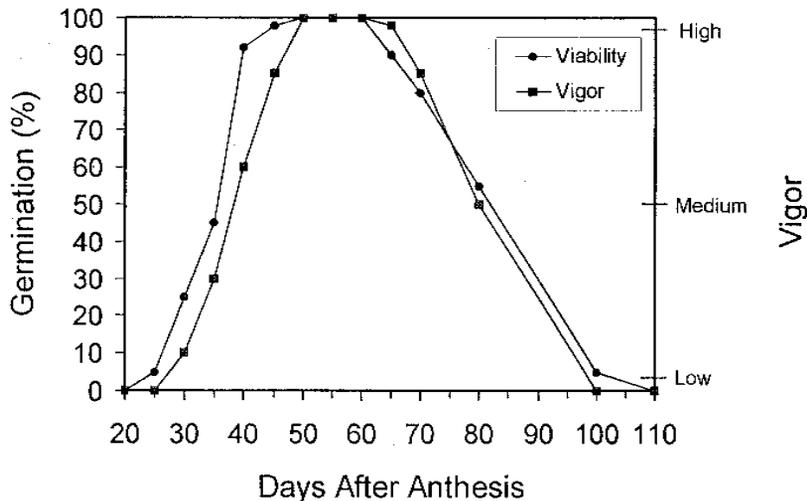
harvested muskmelon seeds until 45 DAA (Fig. 3). Growth of immature embryos of other species often occurred only after maternal tissues surrounding the embryo were removed (Kermode and Bewley, 1988; Symons et al., 1983). Also, post harvest drying stimulated both the viability and vigor of immature muskmelon seeds (Welbaum and Bradford, 1989).

Maternal tissues surrounding the embryo, e.g., endosperm and testa, apparently help maintain developmental metabolism through a combination of physical barriers to expansive growth and endogenous plant growth substances (Welbaum et al., 1998). The endosperm completely encloses and creates tension on the fully hydrated embryo before germination (Welbaum and Bradford, 1990a; Welbaum et al., 1998). In other words, additional expansion and water uptake by fully hydrated seeds only occurs after the endosperm envelope is broken (Welbaum and Bradford, 1990a). When the endosperm envelope is ruptured, the tension is released,

decreasing embryo water potential and creating a gradient for the water uptake that drives expansive growth of the radicle during the onset of germination (Welbaum et al., 1998). This situation is not analogous to hard-coated legume seeds, because for many cucurbit seeds, the testa and endosperm pass water freely and do not provide a significant barrier to water movement into the embryo. The endosperm and, to a certain extent, the testa provide a significant physical barrier to embryo expansion in much the same way a tire limits the expansion of the inner tube inside (Welbaum et al., 1998). The endosperm ruptures because of enzymatic induced degradation of endosperm tissue adjacent to the radicle.

Endo- $\beta$ -D-mannanase is one enzyme putatively responsible for endosperm weakening in a number of species including members of the family Cucurbitaceae (Welbaum et al., 1998). Endo- $\beta$ -D-mannanase activity was low in endosperm tissue of immature 25 and 30 DAA seeds removed from the fruit, dried, and rehydrated for 15 h at 25 °C (Fig. 4). Activity peaked 45 to 50 DAA as seeds reached maximum germinability (Fig. 4). The resistance of endosperm tissue to radicle penetration, as measured using an Instron Universal Testing Machine following hydration for 15 h at 25 °C, increased during seed development (Fig. 5A and B). The turgor pressure of fully hydrated 30 DAA embryonic axis tissue measured directly by psychrometry was 0.6 MPa (6 bars) (Fig. 6). This is 0.2 MPa (2 bars) lower than previously reported for fully mature and germinable 60 DAA seeds, indicating that maximum embryo turgor before germination increased only slightly during development (Fig. 6; Welbaum and Bradford, 1990a). Apparently, the increased enzyme activity and turgor more than compensate for the increased strength of the endosperm tissue allowing viability to increase as the seeds develop (Fig. 3).

Muskmelon seed development is likely under hormonal control as well. Highest concentrations of abscisic acid (ABA) in muskmelon seeds were measured by indirect enzyme linked immunosorbant assay (ELISA) 25 DAA at the point in development when isolated embryo tissues grew only when isolated from the surrounding maternal tissues. The highest concentrations of ABA at 25 DAA were measured in the embryonic axis and endosperm tissue, while cotyledons and testae had much lower ABA contents (Welbaum et al., 1995a, 1999). As seeds developed the ability to germinate, ABA concentrations fell to very low levels in all tissues after 40 DAA, so the development of germinability is well correlated with a decline in endogenous ABA concentrations. Also, im-



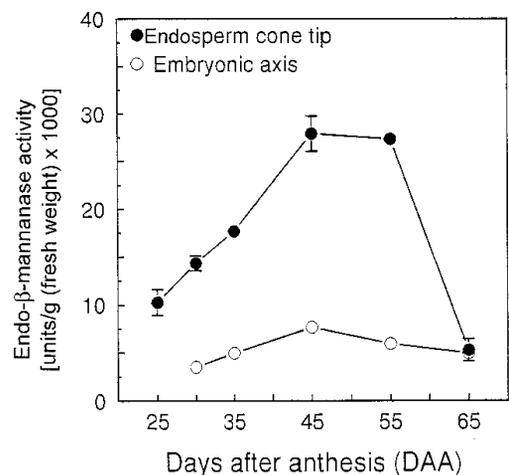
**Fig. 3. Comparison of the development and loss of germinability and vigor of 'Top Mark' muskmelon seeds during seed development and senescence from field research in Davis, Calif., and Blacksburg, Va. Viability tests were obtained using standard and modified Association of Official Seed Analysts germination tests (AOSA, 1988). Vigor is expressed on a relative scale based on germination rate, 4-d root lengths, and tolerance to water stress and exogenous abscisic acid. Data were compiled from Welbaum, 1993; Welbaum and Bradford, 1988, 1989; and Welbaum et al., 1990.**

mature muskmelon seeds are the most sensitive to exogenous ABA early in development when ABA levels were highest in the tissue (Welbaum et al., 1990). Higher levels of endogenous gibberellic acid-like substances in muskmelon embryos were correlated with superior germination under suboptimal conditions, indicating that gibberellic acid (GA) may play an important role in muskmelon seed germination (Edelstein et al., 1995a). Gibberellic acid levels were not measured in developing seeds in this study.

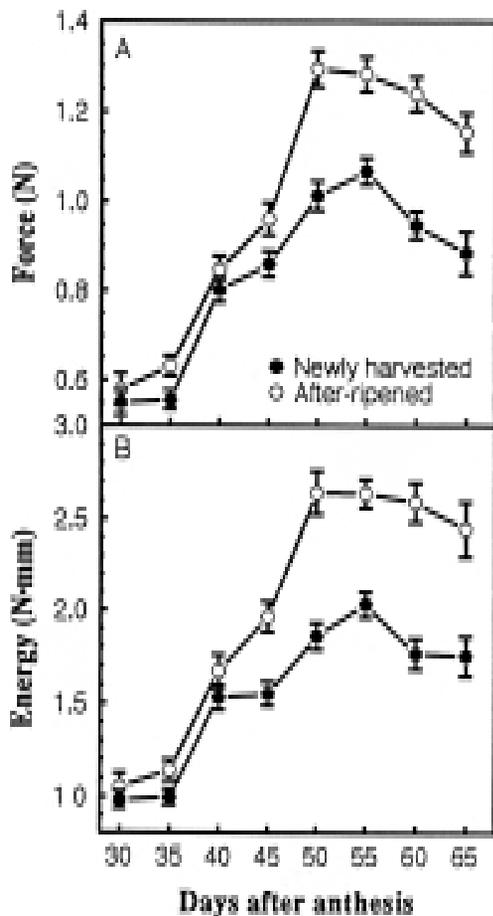
Post harvest washing in tap water for 3 h increased vigor as measured by 4-d root lengths during standard germination testing after harvest. (Association of Official Seed Analysts, 1988; Welbaum and Bradford, 1989). The increased vigor following post harvest washing was still evident after storage for six years under favorable conditions (Oluoch and Welbaum, 1996). It is unknown whether washing increased vigor by leaching inhibitors of seed germination or by some other mechanism. In summary, muskmelon seeds developed the ability to germinate as endogenous ABA decreased, sensitivity to exogenous ABA decreased, turgor increased slightly, mannanase activity increased, and the resistance of the endosperm to penetration also increased.

'Top Mark' Muskmelon seeds reach mass maturity roughly 10 d before edible fruit maturity (Fig. 7). However, precocious seed germination in muskmelon is a relatively rare event even though ABA concentrations are low and the surrounding fruit tissue remains moist during the later stages of development. Muskmelon seeds avoid precocious germination because the accumulation of osmotic solutes, primarily sugars, creates a low water potential inside developing fruit that maintains seed water content below the threshold required for germination (Welbaum et al., 1990). This osmotic inhibition of germination occurs even in the absence of phytohormones because germination is prevented by the low osmotic potential inside the fruit. Precocious germination occurs more frequently in armenian cucumber, which is also *Cucumis melo*, because these fruit accumulate less sugar and, therefore, have a higher (less negative) fruit osmotic potential (Welbaum, 1993).

The optimum harvest time for cucurbit seed crops varies with the environment and cultivar. For muskmelon seeds, maximum viability and vigor in the field were obtained only for a relatively short period (Fig. 3). Under typical conditions in the Sacramento Valley of California, seeds remained 100 % viable for roughly 15 d before a drop in viability was detected (Fig. 3). Maximum vigor in muskmelon seeds, as defined by the rate of germination, developed more slowly than viability (Fig. 3). Vigor remained high at



**Fig. 4. Endo-β-D-mannanase activity in 'Top Mark' muskmelon endosperm cone tips at different stages of development determined by a gel diffusion assay (Downie et al., 1994) after incubation in water for 15 h at 25 °C (77 °F). Each point is the mean of four replicates of eight seeds each. Error bars are ±SE when larger than the symbols. One unit of enzyme activity is that amount that catalyzes the formation of 1 μmol of product per minute.**



**Fig. 5. The force (A) and energy (B) required to penetrate muskmelon seed pieces from eight stages of development following imbibition for 15 h in water. An Instron Universal testing machine (model 1123; Instron Engineering Corp., Canton, Mass.) forced a probe, similar in size and shape to the radicle, through the embryonic axis and tissue adjacent to the radicle to estimate resistance to radicle emergence at different stages of development (Welbaum et al., 1995b). Measurements were made immediately following harvest (closed circles) and after five months of dry storage (open circles). Each point is the mean of three samples of eight seeds each, and error bars are  $\pm$ SE when larger than the symbols;  $N = 1 \text{ kg}\cdot\text{m}^{-1}\cdot\text{s}^{-2}$ ,  $\text{N}\cdot\text{mm}^{-1} = 10^{-3} \text{ J}$ .**

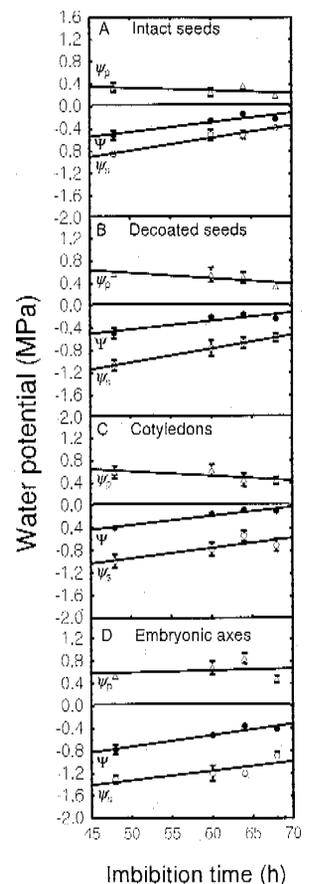
65 DAA as viability began to decline. This is in contrast to traditional wisdom that seed vigor declines more rapidly than viability during deterioration (Delouche and Caldwell, 1960). Both viability and vigor fell rapidly with advanced seed deterioration in the field as predicted (Fig. 3).

Seed to seed variation within a lot is a common problem in many crops including the cucurbits. Variation in performance of commercial lots of muskmelon seed has been attributed to combining many individual fruit from different stages of development into a single lot (Oluoch and Welbaum, 1996).

However, many other factors besides seed age contribute to seed to seed variation. Seeds from each fruit conceptually form an individual seed lot because the position of the fruit on the plant and the environment affect seed quality (Stephenson, 1992). Therefore, pooling many different fruit to create a lot, even if all were from the same stage of development, increased seed to seed variability. Also, it is likely that not all seeds develop uniformly within a single fruit. In squash (*Cucurbita pepo* L.), seeds produced from intense pollen competition (more pollen grains per stigma) were more vigorous and exhibited reduced genetic variation than offspring derived from flowers with little pollen competition (Winsor et al., 1987). In legume fruit, seed position helps to determine the likelihood of abortion, the rate of reserve deposition, and ultimate dry mass (Stephenson, 1992). Seed position inside developing cucurbit fruit likely affects seed development in similar ways.

It is difficult to identify the point of optimal seed quality when harvest should occur. Based on germination rate, low temperature germination, and resistance to controlled deterioration, optimum seed quality occurred when 'Top Mark' fruit are harvested 50 to 55 DAA or  $\approx 10$  d past edible maturity (Oluoch and Welbaum, 1996). This is also  $\approx 20$  d past seed mass maturity. The development of physiological maturation increases seed vigor and continues after seed mass maturity when seeds are already fully viable. Physiological maturation of seeds proceeds quickly inside maturing and senescing fruit because of the high moisture content and high temperatures inside (Welbaum, 1993). This environment also favors rapid aging if seeds are not harvested and dried to slow the

**Fig. 6. Water potential ( $\Psi$ ), solute potential ( $\psi_s$ ), and pressure potential ( $\psi_p$ ) measured for intact 30 d after anthesis (DAA) 'Top Mark' muskmelon seeds (A), decoated seeds (B), cotyledons (C), and embryonic axes (D) in the hours just before radicle emergence. Measurements of  $\Psi$  were made by thermocouple psychrometry on tissues isolated from intact seeds imbibed on water for the times indicated. Solute potential was measured on the same samples after freezing and thawing, and  $\psi_p$  was calculated as the difference between  $\Psi$  and  $\psi_s$ . Values are means of four to eight replications  $\pm$ SE when larger than the symbols. The pressure potential in the embryonic axes of immature 30 DAA seeds just before radicle emergence was  $\approx 0.2$  MPa (2 bars) less than previously reported for mature fully mature and viable 60 DAA axes, indicating that turgor pressure increased only slightly as seeds developed full germinability; 1 MPa = 10 bars.**



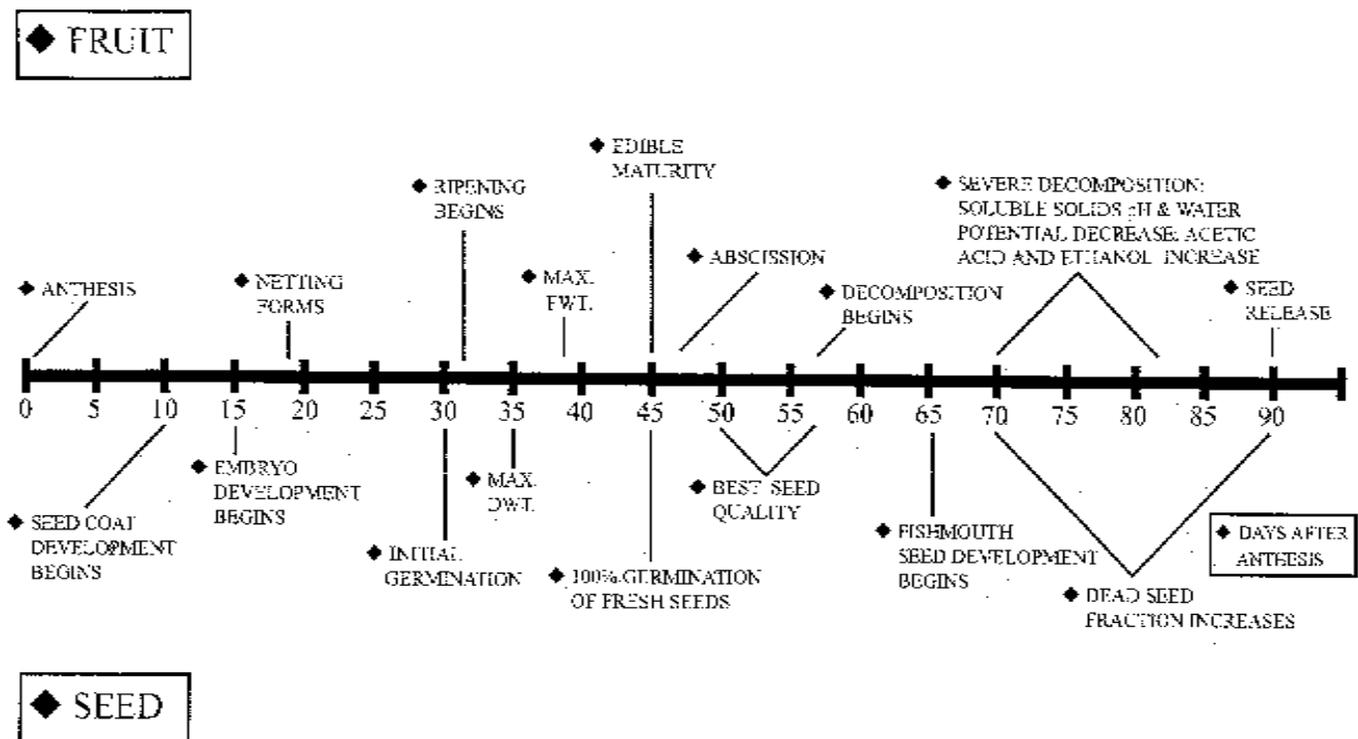
aging process once full physiological maturity has been attained. In the field, the transition from high quality to aged or even dead seeds occurs swiftly over a matter of a few days, particularly at high temperatures (Fig. 3).

'Top Mark' seeds at 50, 55, and 60 DAA germinate rapidly, at low water potentials, at reduced temperatures, and after accelerated aging or long term storage (Oluoch and Welbaum, 1996; Welbaum and Bradford, 1989; Welbaum et al., 1990). In contrast, 65 DAA muskmelon seeds grown under the same conditions showed very high vigor at harvest although a percentage of the seeds had already lost viability in the fruit. After long-term storage or accelerated aging, a significant percentage of these seeds had lower viability and vigor compared to less mature seeds (Welbaum and Bradford, 1991a). The additional 5 d within the fruit caused a fraction of 65 DAA seeds to age beyond peak physiological maturity, reducing seed quality. So delaying muskmelon seed harvest by 5 d significantly reduced seed quality.

For seeds in dry storage, there is a definite threshold on the axis of seed longevity defining the border of seed death (Ellis and Roberts, 1981). This hypothesis applies to mature cucurbit seeds awaiting harvest in the field as well. For 'Top Mark' this threshold appears to be roughly 60 DAA under production conditions in California's Sacramento Valley. Under the

adverse conditions that cucurbit seeds are exposed to in production fields, this threshold is reached faster than seeds that are dried and held in conventional storage. If muskmelon seeds remain inside the fruit until they are released naturally following severe fruit decomposition,  $\approx 90$  DAA, a high percentage of the population will likely be dead (Fig. 2, Welbaum, 1993). The rapid aging of muskmelon seeds in senescing fruit is due to the combined effects of high temperature, low fruit water potential, low oxygen partial pressures, and possibly high carbon dioxide partial pressures. Muskmelon cultivars differ in their sensitivity to anoxia during germination, so certain cultivars may also be more sensitive to the low oxygen environment in decaying fruit than others (Edelstein et al., 1995b). Apparently, years of breeding muskmelon fruit for a tough rind that does not quickly decompose along with high tissue sugar content has impaired the natural reproductive efficiency of this crop. In contrast, armenian cucumber seeds remain viable until the fruit decompose and the seeds are released into the environment (Welbaum, 1993).

A developmental time course for 'Top Mark' seed development and maturation is explained in Fig. 7 based on multiple years of seed production research. The optimum time for seed harvest varies among cultivars, environmental conditions and must be determined empirically for each production area and culti-



**Fig. 7. Descriptive comparisons of 'Top Mark' muskmelon fruit and seed development from anthesis to fruit decay and seed release. Developmental markers are based on data from previous studies of fruit and seed development in California and Virginia (Oluoch and Welbaum, 1996; Welbaum, 1993; Welbaum and Bradford, 1988, 1989; and Welbaum et al., 1990).**

var. Seed crop management techniques, that encourage foliage cover to lower fruit temperatures and allow harvest before severe fruit decomposition occurs, help prevent preharvest losses in seed quality. Once-over destructive seed harvests contribute to variable cucurbit seed quality because immature and over-mature fruit are combined into a single seed lot.

Physiological maturation can also continue while seeds are in the dry state, albeit at a slower rate. In dry seeds, the process is called afterripening and the duration required to achieve maximum vigor varies with cultivar, storage temperature, and moisture conditions. Therefore, muskmelon seed quality may actually improve in dry storage, particularly for seeds harvested between 35 and 50 DAA that have not matured in the fruit. Generally speaking, the higher the moisture content and temperature, the faster afterripening will occur (Welbaum and Bradford, 1991a). At high temperatures and/or moisture contents, afterripening can occur in a matter of hours. Under low temperatures and moisture contents, the process may require months (Welbaum and Bradford, 1991a). The physiological mechanisms responsible for afterripening remain poorly understood.

Seed priming, controlled hydration followed by redrying, may substitute for afterripening by making seeds behave as if they were more mature. The water potential inside developing muskmelon fruit is about  $-1.3$  MPa ( $-13$  bars) and approximately the same as an osmotic priming solution (Welbaum and Bradford, 1991b). Apparently, muskmelon seeds are primed in situ during the later stages of development after seed mass maturity. Therefore, seed lots comprised of immature seeds that are not physiologically mature tend to show a greater response to priming than seed lots comprised of older seeds. Priming can effectively improve the quality of seed lots that were harvested prematurely or that have not reached full physiological maturity (Welbaum and Bradford, 1991b).

When seed aging results in extensive solute leakage, the testae of muskmelon seeds frequently split apart and appear in side view like an open fish's mouth upon full hydration. These dead seeds are frequently termed fish-mouthed or osmotically distended (OD). Muskmelon endosperm is a single suberized cell layer covered with a deposit of callose that is deposited during development around 30 to 35 DAA (Yim and Bradford, 1998). This tissue was incorrectly identified as perisperm in earlier studies (Singh, 1953; Welbaum and Bradford, 1990b). Additional investigation using electron microscopy revealed that the layer putatively identified as perisperm tissue is actually a deposit of callose on the outer surface of the endosperm tissue (Yim and

Bradford, 1998). Fish-mouth seed formation occurs because of the unique semipermeable characteristic of the callose layer associated with endosperm tissue in cucurbit seeds (Welbaum and Bradford, 1990b; Yim and Bradford, 1998). This unique tissue allows water to pass freely but blocks the diffusion of large molecular weight solutes that leak from damaged embryo cells. These trapped solutes attract water resulting in osmotic swelling of the seeds causing the seed coats to split. Cucurbit seed lots frequently contain a high percentage of OD seeds when harvest is delayed and seeds have advanced from physiological maturation into accelerated aging as described above (Fig. 3). Not all dead seeds show the characteristics of osmotic distention. However, all OD seeds are dead.

Overall, cucurbit seed quality in the U.S. is very good. Seed quality could be further improved by applying the results of recent cucurbit seed production and quality research. Seed development in fleshy fruit differs primarily because phase II of seed development is extended over a much longer period of time compared to the more widely studied dry-seeded grain crops (Fig. 1). The prolonged hydration may have adverse effects on seed quality under high temperature and other adverse conditions (Welbaum, 1993). Also, many cucurbit seed crops have been bred for longer shelf life and, in the case of the melons, higher sugar content which may also negatively affect seed development (Welbaum, 1993). As a consequence, the time of seed harvest in these crops is critical for achieving the best possible seed quality. Unfortunately, there is no simple formula that can be followed for determining the best time to harvest seed crops for all the cucurbits. Research has shown that muskmelon seed crops should be harvested before the onset of severe fruit senescence to prevent aging of the seeds inside (Fig. 7). Priming can advance the maturity of immature seed lots that were harvested prematurely (Welbaum and Bradford, 1991b). However, priming will not restore lost quality to seed lots subjected to preharvest seed aging caused by delayed harvest (Oluoch and Welbaum, 1996). A once-over destructive mechanical harvest is frequently used commercially for open-pollinated cucurbit seed crops but combines seeds from many stages of development into a single lot. Combining seeds from different stages of physiological maturity in this way may adversely affect quality and increase seed to seed variability. Hand harvesting cucurbit fruit at the optimal stage of development could improve seed quality in many cases. However, hand harvesting is a more costly and time-consuming practice that would increase seed production costs.

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