The concentration of seed production for some crops in specific areas of the U.S. and of other countries is persuasive testimony of the influence of environmental factors on seed development and quality. The environmental factors that have contributed to the selection and establishment of these specialized seed production areas can be sketched in rather broadly in brief reviews of some of the areas.

Specialized seed production areas

A major portion of the seed of temperate climate forage and lawn/turf grasses is produced in the Pacific Northwest, especially in Oregon. The seed produced in this area is supplied to other parts of the U.S., especially the eastern half of the country, to many countries in Europe and to Japan. Climate and other components of the environment are favorable for production in the Pacific Northwest for forage and forage legume seed (23, 62). Perhaps, the most important factor is the dry summer season. The seed complete maturation, dry down, and are harvested with little risk from rain and wind. Other favorable factors in the area are mild winters with little winter killing, ample rainfall for good growth, and a variety of soil types suitable for different species. The establishment of forage and turfgrass seed production in the Pacific Northwest resulted in the development of several other factors which now contribute to the continued success of seed enterprises in the area: effective, relevant research and service programs, and a corps of experienced seedsmen.

The arid, irrigated areas in California, Idaho, Arizona and other western states are important producers and suppliers of vegetable, flower, and forage legume seed. Low humidity, minimal rainfall, and favorable temperatures reduce the spread of seed borne diseases as well as the risks associated with inclement weather during the late maturation and harvest periods. Good soils, controlled moisture supply through irrigation and bright sunny weather contribute to stability of production, high yields, and high quality of the seed produced. Again, progressive research programs and professionalism of the seedsmen also contribute to the dominance of arid, irrigated areas in seed production.

The production of seed of dry, edible beans and snap beans provides a more specific illustration of the favorableness of arid, irrigated areas for seed production. The bacterial blights of beans are destructive diseases in the warm, humid Upper Great Lakes region where commercial production is concentrated. The diseases are seed borne and infected seed are an important source of inoculum for their spread (13). Production of seed under irrigation in arid areas in Idaho and California combined with stringent quarantine and blight prevention programs permit the production of blight-free seed. The seed are marketed to gardeners and commercial producers and to seed producers in the Upper Great Lakes area for further multiplication under certification.

Arizona is rapidly becoming a major supplier of cotton seed for the Mid-South and Southeastern cotton belt. Production of cotton seed in the humid cotton belt has always been risky and the quality of the seed produced is seldom better than mediocre (59). The increasing severity of the economic consequences of poor stands and stand failures resulting from the interaction of low seed quality and adverse climatic conditions at planting time has created a demand among cotton planters for high quality seed. Fortunately, Arizona plants some of the same varieties of cotton as the humid cotton belt. The seed are usually high in vigor because there is little if any weather-eraging during the period between bolt opening and harvest. During the past 2 years the production of certified cotton seed in Mississippi has decreased by about 30% and many seed companies in the Mid-South and Southeast are contracting seed production in Arizona.

In the case of seed production for such crops as the cole crops, relatively low temperatures and rather specific photoperiods are required for good, uniform seed stalk formation. Seed production, therefore, is located in areas where these requirements can be met and where other favorable conditions exist, such as the absence of rainfall during the maturation and harvest periods. The U.S. is large enough and has a sufficiently diverse climate to permit establishment of seed production in near optimum areas. Small countries with a more homogenous climate are not so fortunate and have to depend on others for their supply of seed of cole and similar crops.

Although low humidities are generally favorable for seed production, there are exceptions. Hawthorn and Pollard (29) cite the location of some flower seed production in California in areas adjacent to the ocean where humidity tends to be high rather than low at harvest time. The relatively high humidity at harvest time reduces the amount of shattering and seed loss.

The climatic components of the environment are probably the most important determinants in the location of seed production. In some cases, however, other aspects of the environment can be of equal or greater importance. For insect pollinated crops, an abundance of pollinators is essential for good seed set. Sweet corn seed are produced in Idaho because yields are good but also because the production can be isolated from cross pollination with field corn.

India is the only major producer of hybrid cotton seed (41). In 1978-79 enough hybrid cotton seed were produced to plant 750,000 ha. The important factor in India's hybrid cotton seed production is an abundance of low-cost labor for hand pollination and individual boll harvest. Difficulties in pollination provide the major obstacle to the development of hybrid cotton in the U.S. Hand labor is too costly, and insect pollinators do not thrive in the chemical environment produced by cotton insect control programs. China is producing substantial quantities of hybrid rice seed, utilizing a laborious procedure of pollination (the pollen is neither carried by insects nor wind blown).

The location of seed production for hybrid flower and vegetable crops, initially in Japan and Taiwan, and more recently in India and countries in Central America, has been largely determined by the abundance and low cost of hand labor for controlled pollination.

This brief excursion through some specialized seed production areas points up the importance of climate and other components of the environment, such as pollinating insects, isolation from other crops, and abundant low-cost labor. The successful establishment of specialized seed production areas in any country is also dependent on the effectiveness and efficiency of the communications and transportation systems.

The advantages of producing seed in areas especially adapted to seed production are: seed yield set and recovered in harvesting is high and relatively stable; seed germination and vigor are consistently high; and seed-borne diseases can often be avoided or are more easily controlled. Yet, not all kinds of seed are produced in areas with highly favorable environments. Indeed, most of the seed used in crop production in the U.S. are produced in the same areas where the commercial crop is grown, e.g., field corn, wheat, soybeans. Environmental conditions in these areas range from bad to good for seed production. There are always risks and years when seed quality is poor. The remainder of this paper will focus rather selectively on more specific environmental effects on seed quality in non-specialized production areas.

Soil Fertility and Moisture Supply

Plants have evolved a remarkable capacity to adjust seed production to the resources available. The typical response of plants to low soil fertility and/or chronic moisture stress is reduction in the quantity of seed produced rather than in their quality. The few seed produced under environmental conditions are usually as viable and vigorous as are seed produced under more favorable conditions. From an evolutionary viewpoint, the adjustment of seed production to available resources has survival value. A few high quality seed have an equal or better chance of surviving environmental hazards, germinating and developing into at least one plant to continue the species as a greater number would be produced.

Although the broad brush statements above are generally valid, there are exceptions. Harrington (27) produced plants of carrot, lettuce and pepper through the seed production stage in sand cultures under severe moisture and nutrient stress.
with complete nutrition or deficiencies of N, P, K and Ca. The deficiencies were of a degree to produce severe symptoms but not to prevent seed production. While each deficiency depressed yield, only Ca deficiency caused a reduction in germination of carrot and pepper seed. In summarizing his review of the effects of environment before harvesting on viability of seed Austin (2) concluded that, "mineral deficiencies in seed are likely to be rare and the consequences for yield even more rare."

While mineral deficiencies in seed are rare, they do occur and can influence the yield of the crop produced by the seed under certain conditions. Leggatt (35) demonstrated that pea seed harvested from a boron deficient area produced abnormal seedlings when grown in soil and/or dust from dust or borax to the sand; corrected the condition. Soybean seed produced in areas with good molybdenum status can have a Mo concentration sufficiently high to obviate the need for seed treatment with sodium molybdate for planting in Mo deficient soils. (28).

Cox and Reid (14) identified 2 types of concealed damage in peanut kernels associated with boron and calcium concentration in the kernel: discoloration of the cotyledons associated with boron deficiency, and discoloration of the plumule associated with calcium deficiency. Both types of damage were corrected by application of the specific element. The application of 561-785 kg/ha (500-700 lb./acre) of gypsum to large seeded peanuts (Virginia type) at early bloom stage is standard practice (63). Yield is increased and the incidence of "pops" and unsound kernels is reduced. More recently, Sullivan (58) identified 2 additional seedling abnormalities in peanuts associated with low calcium levels: watery hypocotyl and physiological root breakdown. Application of gypsum corrected both types of abnormalities.

High protein cereal seed. High protein cereal seed, especially wheat, often perform better than low protein content seed of the same variety. Fox and Albrecht (21) associated rapid germination and vigorous seedlings with high protein content in samples of wheat seed collected in Nebraska. High protein content, in turn, was associated with N fertilization. Other workers have also demonstrated that N fertilization increases protein content of the wheat grain (9, 19, 22, 23). High positive correlations have been reported between high protein content in wheat seed and energy charge (22), germination percentage (32), seedling vigor (36, 37, 38, 51) and yield of the crop produced from the seed (9, 52).

Seed size. Levels of soil fertility and moisture supply and perhaps of other environmental factors influence seed size and seed weight. There is abundant evidence that there is an association between seed size and/or seed weight and germinability and vigor (2, 3, 26, 30, 36, 40). The degree and structure of the association and its practical significance, however, are poorly understood. Much of this lack of understanding can be attributed to the array of methods used by different investigators to quantify seed size, seed weight and seed density. In many cases the performance of seed of different "relative" seed size and/or seed weight and/or variety classes without documentation of the dimensional or weight characteristics of the population from which the specific classes compared were taken.

Hanumaiah and Andrews (26) compared the germination, vigor, seedling growth rate, plant development and yield of Wisconsin All Season' cabbage and 'Purple Top' turnips grown from small, medium, and large seed. The sizes of each class were given in terms of whether they passed through a series of hand sieves. However, the proportion from which the specific classes compared were taken.

Hanumaiah and Andrews (26) compared the germination, vigor, seedling growth rate, plant development and yield of Wisconsin All Season' cabbage and 'Purple Top' turnips grown from small, medium, and large seed. The sizes of each class were given in terms of whether they passed through a series of hand sieves. However, the proportion from which the specific classes compared were taken.
It is not clear why the small seed in a population are inferior in quality. Most workers have been careful to remove obviously immature seed before sizing. Seed in the small size classes, therefore, do not appear to be immature, e.g., misshapen, shriveled. They are as well shaped and filled out as the large seed. Research is very much needed to test the validity of the conclusions of Aguiar and Wetzel on other kinds of seed, and to determine the cause(s) of inferior quality of the small seed in seed populations.

**Climate during seed development**

The nutritional and moisture deficiencies discussed in the previous section were of the chronic type, i.e., conditions that are marginal for all or a substantial portion of the growing season. Acute deficiencies in moisture supply resulting from temporary but severe drought can have disastrous effects. A drought during the seed development period usually interrupts seed development and results in light, shriveled seed. Once seed are set, many crops have little capacity to adjust seed number to the available resources. A few crops such as cotton can, to some degree, adjust to acute shortages of resources by shedding young fruit.

The environment during seed development and maturation can influence the degree of dormancy of the mature seed. Koller (33) showed that warm temperature during the maturation of 'Grand Rapids' lettuce seed reduced dormancy. Alfalfa seed produced under cool temperatures were heavier and had a high percentage of hard seed. Koller reported that cooling of one cultivar ('Ranger') was also higher when the seed developed and matured under cool conditions.

Cool temperature, especially at night, during the boll development period in cotton delays development and maturation of the young fruit in the "top" crop. Defoliation of the crop to promote opening of the mature fruit and facilitate harvest, terminates the maturation process in immature fruit and forces them to open. The immature cotton seed are low in quality and density but about the same size as mature seed. They can only be separated from mature seed with a gravity separator after the seed have been acid delinted—a process that has been extensively used in the Southeast only in the last 10 years.

A heavy early freeze is a serious hazard in the production of inbred and hybrid seed of corn. The degree of injury or reduction in quality of the seed is related to seed moisture, intensity and duration of the freezing temperatures (15). Rossman (54) concluded that in addition to seed moisture content, temperature, and period of exposure, genotype, husk protection and rate of drying after freezing also influence the degree of quality reduction in corn seed from freezing.

**Weathering: postmaturation—preharvest environment**

Seed attain physiological maturity at moisture contents ranging from 32–55% (e.g., corn, sorghum, rice) to 50–55% (e.g., soybeans, peanuts, beans, cotton). Following maturation the seed (in "dry fruits") continue to dry down until they reach harvest maturity, i.e., the moisture content at which they can be effectively threshed with mechanical harvesters. Climatic conditions during this postmaturation preharvest period have a great influence on the quality of the seed harvested.

Deterioration of seed during the postmaturation, preharvest period is a serious seed production problem in the eastern half of the U.S. Frequent rainfall, combined with high temperatures, results in rapid losses of viability and vigor of seed in standing crops.

Simpson and Stone (55) demonstrated a negative correlation between the viability of cotton seed exposed (open bolls) in the field and the amount of rainfall during the exposure period. Losses of 20 to 30% in viability were common after only 1-week's exposure to rainy conditions. Rainfall during the period that open cotton bolls are exposed before harvest causes a deterioration in oil milling quality as well as viability (45). The quality of the lint is also lowered (8).

Caldwell (7) made a detailed study of field deterioration in cotton seed and established a relationship between the viability and vigor of cotton seed and the period of exposure to high temperature, rainfall and relative humidity before harvest. The seed from bottom bolls which open first and are exposed to the field environment longest before harvest were consistently lower in quality than those from bolls produced in the upper half of the plant. High rates of nitrogen fertilizer, irrigation, narrow row spacings and other practices which contributed to a dense canopy and high humidity within the

---

**Table 3. Seed size distribution and germination percentage of the size classes for 6 lots of 'Bragg' soybeans produced in 4 states in 1972 from (1).**

<table>
<thead>
<tr>
<th>Lot no.</th>
<th>State</th>
<th>Criterion</th>
<th>4.4 mm</th>
<th>4.7 mm</th>
<th>5.2 mm</th>
<th>5.6 mm</th>
<th>Seed diameter (mm)</th>
<th>5.9 mm</th>
<th>6.3 mm</th>
<th>6.8 mm</th>
<th>7.1 mm</th>
<th>Unsized</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>South Carolina</td>
<td>Distribution (%)</td>
<td>0</td>
<td>2.4</td>
<td>16.9</td>
<td>46.2</td>
<td>26.3</td>
<td>6.9</td>
<td>1.3</td>
<td>0</td>
<td>92.0</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>South Carolina</td>
<td>Distribution (%)</td>
<td>0</td>
<td>5.1</td>
<td>20.9</td>
<td>42.8</td>
<td>24.0</td>
<td>6.2</td>
<td>1.0</td>
<td>0</td>
<td>90.0</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Texas</td>
<td>Distribution (%)</td>
<td>0</td>
<td>88.5</td>
<td>89.5</td>
<td>93.5</td>
<td>92.5</td>
<td>87.0</td>
<td>84.0</td>
<td>0</td>
<td>90.0</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Texas</td>
<td>Distribution (%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.0</td>
<td>5.1</td>
<td>27.5</td>
<td>45.3</td>
<td>21.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Louisiana</td>
<td>Distribution (%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.2</td>
<td>6.3</td>
<td>32.1</td>
<td>46.0</td>
<td>14.4</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Mississippi</td>
<td>Distribution (%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>87.0</td>
<td>97.0</td>
<td>92.5</td>
<td>95.5</td>
<td>89.0</td>
<td>94.0</td>
</tr>
</tbody>
</table>

The diameters are equivalent to 1/64 through 18/64 inch.

---

**Table 4. Yield of plants grown from seed of the same relative diameter from large-, medium- and small-seeded lines of soybeans, from (49) and (61).**

<table>
<thead>
<tr>
<th>Relative size class</th>
<th>Yield (bu/acre)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean + 0.79 mm</td>
<td>3.46a</td>
</tr>
<tr>
<td>Mean</td>
<td>3.43a</td>
</tr>
<tr>
<td>Mean - 0.79 mm</td>
<td>3.09b</td>
</tr>
</tbody>
</table>

*Mean separation by Duncan's multiple range test, 5% level.*

---

**Fig. 1. Seed size distribution in 3 nearly isogenic lines of soybeans differing in seed size (small, medium and large seeded lines). X indicates the mean seed size in each population (1/64 inch = 0.4 mm), from (61).**
canopy increased the degree of deterioration of the seed. These results have been confirmed and extended (59, 64). Seed quality problems in cotton associated with unfavorable weather during the preharvest period in the humid cotton belt are the main reason for the shift in cotton seed production to Arizona and other arid areas.

Soybean seed are produced in areas where the crop is grown. Adverse weather conditions during the preharvest period cause moderate to severe seed quality problems in some states or areas within states every year (16). Delayed harvest of soybean seed caused by inclement weather results in a reduction in viability and an increase in mechanical damage during harvest (25). In a study on the effect of planting and maturity dates on soybean seed quality, Green, et al. (24) found that soybean plants from early planting dates which matured seed during hot, dry weather produced seed of reduced quality. Seed from later dates of planting which reached maturity after the hot, dry weather conditions had ended, were high in quality.

Mondragon and Potts (42) and Burdett (4) have studied the deterioration of soybean seed in the field under natural and "modified" conditions. The former reported that seed subjected to ambient environmental conditions in the field declined significantly in germination 4 weeks after physiological maturity (about 50% moisture). Reducing the incident sunlight on the plots by 50% by use of wire screens reduced the temperature and rate of deterioration.

Burdett (4) worked with mid-season ('Dare', Group V) and full season ('Bragg', Group VI) cultivars of soybeans. Various weathering treatments were initiated when the seed had dried down to below 20% moisture (harvest maturity). The treatments consisted of exposure to ambient conditions in the field, ambient conditions plus once and twice weekly sprinklings with 2.5 cm water, and removal of whole plants from the field at harvest maturity to an open-sided shed. The degree of field deterioration that led to a decrease in germination varied among years (1973 and 1974) and depended on the amount of rainfall and the temperature during the exposure (Fig. 2). The supplemental sprinklings increased the rate and degree of seed deterioration relative to ambient conditions. Seed quality was maintained at a very high level on the plants removed from the field and placed under a shed. Burdett attributed this result to protection from rain and a slightly cooler temperature of the seed on these plants. Seed of the mid-season cultivar, which reached harvest maturity about September 24, were more severely affected by the weathering treatments than the full season cultivar which reached harvest maturity about October 20. Burdett concluded that early and mid-season cultivars were more susceptible to seed deterioration because the temperature is usually warmer in late September and early October than in late October, and not because they are inherently predisposed to deterioration.

Some cultivars of soybeans do appear to be inherently more susceptible to field deterioration than others. Lasim (34) compared the rate of field deterioration of 'Dare', 'Mack' and 'Forrest' soybeans, which reach physiological and harvest maturity about the same date. Seed of 'Mack' decreased much more rapidly in germination than those of 'Dare' or 'Forrest' (Fig. 3). The poor weathering resistance of Mack soybeans is well known to seedsmen in Mississippi.

A rather dramatic example of the adverse effect of weathering on seed quality was reported by Oropenza (46), 'Magnolia' cowpea seed attained physiological maturity 19 days after flowering (in August). Moisture content was 50% and germination 98%. Two days later germination dropped to about 94%, and 4 days later it was 65% (Fig. 4). Rainfall at about the time the seed reached physiological maturity and continuing for several days combined with high August temperatures caused this rapid reduction in quality of the seed. The incidence and severity of fungal invasion of seed is increased by weathering (43, 44, 53). The old question of whether fungal invasion is a cause or consequence of deterioration is not yet completely resolved.

Weathering is a major problem in seed production. The severity of weathering and the limitation imposed on seed quality by weathering generally increases from cool to warm areas. The worst situation is in the humid subtropics and tropics. The quality of seed produced is generally low and deterioration continues at a rapid rate during storage because of high temperatures and humidities.

**Protection from the environment**

A long term concern of seedsmen is protection (of seed) from the environment. There is variation among crop species for resistance to weathering, but plant breeders have given scant attention to the development of weathering resistant lines or cultivars. Indeed, it appears that plant breeders have unconsiously and indirectly selected for lessened resistance to weathering: e.g., thinner seed coats, minimal dormancy.

Dormancy provides the natural protection against seed deterioration while seed are still on the plant and after they are dispersed. Dormancy is generally perceived as a mechanism for delaying and distributing germination over time. There would be little survival value in dormancy, however, if it did not also reduce the rate of deterioration in seed so that germination also is distributed over time. Dormancy, however, is a nuisance in annual cropping systems and man (including breeders) has selected for reduced dormancy in most major crop species. In some lines (and cultivars) dormancy has been reduced to such a low level that germination on the plant is a serious problem.

There is considerable current interest and research on dormancy as a means of reducing the adverse effects of weathering on seed...
Christiansen remarkably stable in moisture content after they dried down to below 15% (Table 5), and they maintained germination in the field for much longer than the cultivars planted in Mississippi. The progress of field deterioration of seed of the D67-5677-1 line and of the closely related ‘Dare’ cultivar are shown in Table 6. The hardseeded line is not without problems. Combining greatly reduces but does not eliminate hardseediness. Seed of the hardseeded line lost during combining volunteer vigorously the following spring and summer. Despite these problems, the hardseeded character should be very useful in soybean cultivars developed for the humid subtropics and tropics.

There is evidence that seed dormancy in other species is useful in maintaining seed quality. Plant breeders should certainly give more attention to the potential of dormancy and other characters for facilitating the production of high quality seed.

### Summary

The environment has considerable influence on the development and quality of seed. The production of seed of many crops has shifted to areas in the U.S. and other countries where conditions are more favorable for seed production than in the areas where the crops are grown. Arid, irrigated areas, or areas with a distinct dry season during the late maturation and harvest periods are favorable for seed production. Production of seed in specialized areas has—until now—been largely confined to high value seed (ornamentals), crops produced for parts other than the seed (many vegetables, forages), and for crops in which seed-borne diseases are a major problem (beans). The bulk of the corn, wheat, and soybean seed is still produced in the commercial production areas, where environmental factors can be unfavorable for seed production. Plant breeders need to give more attention to incorporating resistance to unfavorable conditions, into cultivars of acceptable types.

### Literature Cited


780