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Vegetable Soybean and Its Seedling Emergence in the United States

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Abstract

Vegetable soybean or edamame is a specialty soybean (*Glycine max* (L.) Merr.). Unlike grain-type soybean (mainly for oil and source of protein in animal feeds), edamame pods are harvested at a green and immature stage, and beans are consumed by humans as a vegetable. While originally from China, edamame has recently gained much-increased popularity and expanded market needs in the US. However, domestic edamame production is limited in the US because at least 70% of the edamame consumed is imported. Poor seed germination and seedling emergence are one of the major problems in US edamame production. This review focuses on the introduction of edamame, a high-value niche crop, and its low emergence issue in production. Here, we provide a comprehensive exploration of the factors that influence edamame germination and emergence, including the intrinsic factors related to seeds (seed and seedling characteristics), and extrinsic factors related to the biotic (soil/seed-borne diseases) and abiotic (seedbed physical components as well as their interaction with climate) stresses. This information will help farmers and plant breeders to better understand the causes of the poor edamame emergence and may provide a foundation for improved field management of edamame, to increase production of this valuable specialty crop.

Keywords: vegetable soybean, seedling emergence, seed vigor, biotic stresses, abiotic stresses

1. Introduction

Vegetable soybean is a specialty soybean (*Glycine max* (L.) Merr.). Unlike grain soybeans (mainly for oil, source of protein in animal feeds, and processed foodstuffs, including soy sauce, tofu, soy milk, and natto), vegetable soybeans are consumed by humans as a vegetable [1]. Originating from China, vegetable soybean is popular throughout East Asian countries (especially China, Japan, and Korea) due to its long history of consumption. The earliest documentation of vegetable soybean comes from poems by Lu You (1125–1210 AD), a distinguished scholar in China, describing the picking and eating of green soybean pods. Vegetable soybean is commonly called “maodou” among Chinese people [2]. In 1275 AD, the popular name “edamame” appeared in Japan, and a well-known Buddhist Saint Nichiren wrote a note thanking a parishioner for the edamame he left at the temple [2]. Now, edamame, which literally means “stem bean” (eda = “branch” or “stem” and mame = “bean”), is commonly used to refer to vegetable soybean in many countries [3].

Soybean development and maturation can be divided into vegetative and reproductive physiological stages. The vegetative stages are numbered according to how many fully developed trifoliate leaves are present, including emergence (VE), unrolled unifoliate (VC), and a series of stages named by the number of leaves (V1–V(n)) [4]. The reproductive stages are characterized by blooming (R1 and R2), pod development (R3 and R4), seed filling (R5 and R6), and plant maturity (R7 and R8) stages [5]. Unlike grain soybeans that are harvested at full maturity (R8 stage), edamame is harvested in pods between the reproductive stages of R6 and R7, when beans fill 80–90% of the pod width and still retain around 65% moisture content [6]. Harvesting at the R6 stage brings the benefits of having desired edible quality attributes for edamame, such as peak seed weight and sucrose content, lower oligosaccharide and anti-nutrients values, and intense green color [7]. Loss of quality occurs as pods turn yellow; therefore, harvest time is very important in edamame production [8]. Characteristics for high-quality edamame pods are bright green crescent-shaped pods (approximately 5.0 cm in length and 1.4 cm in width) with light pubescence (white to gray) and unblemished pods containing two to three large seeds (seed dry wt >250 mg/seed) with a hilum consisting of a buff or yellow color [9–11]. Edamame varieties can possess different seed coat colors, ranging from yellow, green, brown, or black [12]. For the best quality, seeds should have a smooth and firm texture (but not chewy), higher sugar content (especially sucrose), and distinctive flavors (such as sweet, nutty, buttery, and beany flavors) [13, 14].

In the past few decades, globalization has provided a platform for international edamame trade and allowed more people to enjoy its unique taste well as multiple health and nutritional benefits. Now, edamame is becoming more and more popular all over the world, particularly in the United States.

1.1 Nutritional and functional values

Edamame can be considered a nutraceutical and functional food crop. The nutritional value of edamame is mainly determined by its chemical constituents, such as protein, fiber, starch, and sugars. Compared to grain soybean, edamame has lower oil, lower trypsin-inhibitor levels, fewer indigestible oligosaccharides, and more vitamins [12]. Since edamame is a complete protein source containing all the essential amino acids associated with human health, it is usually considered an alternative to meat and can support vegan, vegetarian, and other plant-based diets by providing viable and more environmentally friendly proteins [15].

Edamame also has superior nutritional content when compared to green peas [16]. Masuda reported that the calorific value (energy) of edamame is about six times that of green peas; edamame bean contains 60% more Ca, and twice the P and K of green peas; the Na and carotene content of edamame is about one-third that of green peas and they have similar quantities of Fe, thiamin (vitamins B1), and riboflavin (B2) [17]. In addition, edamame is a rich source of vitamins A, B1, B2, vitamins C (ascorbic acid), vitamin E (tocopherol), niacin, and health-promoting polyunsaturated fatty acids, such as linoleic acid and linolenic acid [18, 19]. Edamame also contains a significant amount of dietary fiber, which when consumed in sufficient quantities could help to reduce blood cholesterol levels due to its viscosity, solubility, and ability to bind molecules [20].

Moreover, edamame is also regarded as a functional food, mainly because of the presence of phytohormones called isoflavones that are associated with the prevention of several human diseases. The major isoflavones present in edamame are genistein and daidzein [21]. Clinical studies show that they have a positive influence on increasing HDL cholesterol (considered good cholesterol) and lowering LDL

cholesterol (bad cholesterol), reducing the risk of cardiovascular diseases [22]. Isoflavones have also been reported to have a preventive effect on other diseases, such as breast cancer, diabetes, menopausal symptoms, and osteoporosis diseases [21]. However, Roland et al. reported that soybean isoflavones may be associated with astringency and bitterness, two undesired sensory attributes that can impact edamame quality [23]. Some studies also observed the health benefits of edamame seed coat pigments. For example, black and brown seed coats accumulate anthocyanins and procyanidins, two antioxidants that could aid in fighting cardiovascular disorders, preventing inflammation, and scavenging harmful radicals [24–26].

1.2 Versatility as a food ingredient

Vegetable soybean can be either sold fresh as pods on the stem, stripped pods, shelled beans, or sold as frozen or canned products. It is versatile as a food ingredient routinely found in salad bars, stews, soups, stir fry dishes, and sushi restaurants as appetizers, as well as an ingredient in hummus or healthy snacks. Edamame is quite easy to prepare as a snack. Pods are usually lightly cooked in salted/unsalted boiling water for 5–7 min and then the beans can be pushed directly from the pods into the mouth with the fingers [27]. Edamame beans can also be roasted like peanuts. Additionally, some companies use edamame to prepare innovative products, such as processed edamame sweets and desserts, green milk, green tofu, green noodles, and soygurt [27, 28].

1.3 Economic importance in the US

Consumers' widespread appreciation of edamame's benefits has resulted in a dramatic growth in demand for edamame in the US since the early 2000s. Sales of edamame in the US increased from 18 million USD in 2003 to 30 million USD in 2007 and reached 84 million USD in 2013 [29]. Today, edamame is the second-largest soy food in the US with about 30,000 tons consumed annually [7]. Edamame is readily available in the US, found in supercenters (e.g., Walmart), grocery stores (e.g., Kroger and Food Lion), wholesale outlets (Sam's Club and Costco), farmers markets, and local restaurants [30].

It is reported that 70% of edamame consumed in the US is primarily imported frozen from China, which is the largest producer, consumer, and exporter of edamame in the world [31]. Frozen-processing methods used by commercial processing facilities may lower edamame quality drastically [32]. Some studies also reported the introduction of harmful foodborne bacteria, such as *Escherichia coli* and *Listeria monocytogenes*, during processing that cause human illness [33]. With the raising concerns about the safety of imported edamame, consumers are seeking domestically grown edamame. This expanding domestic demand, especially for local fresh edamame, has stimulated interest among plant breeders, growers, and food processors in edamame production in the US.

The US is known as one of the top grain soybean-producing countries in the world with ~30-million-hectares grown each year, valued at more than \$40 billion [34]. Compared with grain soybean, edamame is grown on a much smaller scale but has a greater market and economic value. Edamame is a profitable alternative crop, especially for small-scale farmers and urban agriculture growers, seeking to increase income by growing a high-value niche crop [30]. First, farmers can adopt edamame production easily, since edamame shares similar production practices with grain soybeans, such as fertilization and irrigation [5]. Second, farmers can get higher gross returns, because edamame has relatively low startup costs, higher market prices as a specialty vegetable, and large local market potential. It is reported

that the net returns reached \$4940–\$5434/hectare of land in some parts of the US [35], and a report from Mississippi showed that the net return of edamame could be more than twice the returns from grain soybean production [8]. Third, edamame can serve as a component of crop rotations and diversify crop production for US growers. Edamame can fix atmospheric nitrogen and can be used in the ubiquitous wheat/corn-soy rotations which have benefited US growers for many years. Finally, since organic farming gains increased popularity now with the raising public awareness of the environment and human health, organic farmers may benefit from planting edamame based on its high nutritional and market value.

All of these have resulted in a steady increase in land acreage under edamame in the US. However, edamame production faces some challenges and problems, such as limited genetic resources, poor seedling establishment, lodging, inferior plant structure, susceptibility to seed diseases, low yield potential, and greater perishability compared to grain soybeans [30]. From the standpoint of farmers, poor seedling establishment is considered a critical issue that needs to be solved. Seed germination and seedling growth is the first step in establishing a successful crop. Successful stand establishment eliminates the need for replanting and determines the success or failure of the future harvest.

2. Emergence issues in edamame production

Poor emergence is a common problem in field research for edamame and has been well documented in the literature. Williams reported average emergence below 35% among 136 diverse edamame cultivars [34], which is much lower than a normal plant population (80%) for commercial grain soybeans [18]. Poor crop emergence has also been observed in edamame field trials in many states in the US, including North Dakota, Georgia, Illinois, Pennsylvania, and Virginia, where emergence percentages range from 60 to 85% for different cultivars [18, 36, 37]. Poor emergence influences yield if the plant density is below a critical level. To ensure successful stand establishment under variable field conditions, even when using high-quality seeds, good field management practices are needed for edamame.

Up to now, there is still little known about growing edamame in the US. Most planting decisions are based on grain soybean recommendations. However, edamame differs from grain soybean seeds in several key characteristics, such as larger seed size, which may indicate that not all grain soybean management decisions can be applied to edamame. Edamame emergence has been reported to be highly variable among genotypes, indicating the importance of genetics and seed vigor on seedling establishment. Recent studies also reported that edamame emergence was influenced by several factors, such as seed size, plant depth, and temperature [18, 38–40]. Scientific research publications on edamame emergence are still limited. However, related studies on grain soybean establishment may help us to understand issues surrounding edamame field emergence. In this chapter, we discuss edamame seedling emergence, as well as the factors influencing edamame germination and emergence, including both intrinsic factors related to seeds (seed and seedling characteristics) and extrinsic factors related to the biotic (soil/seed-borne diseases) and abiotic (seedbed physical components and their interaction with climate) stresses in the environment.

2.1 Seed emergence process and critical edaphic factors (soil moisture, temperature, and oxygen) involved

Stand establishment is the most important and vulnerable phase of a crop cycle. High-quality seeds require three appropriate conditions for germination—soil

moisture, temperature, and oxygen [41]. Temperature and water availability are two crucial factors that drive the rate of progress through seed imbibition, germination, and seedling growth to emergence [42]. Soybean seeds need to imbibe at least 50% of their mass water to germinate. Edamame has a larger seed size than grain-type soybean, making them more susceptible to soil water stress since they need more water to fully imbibe. Their larger seed size also requires more time to fully hydrate. Seeds will germinate slowly or fail to germinate if the soil moisture is inadequate. Optimally, seed imbibition can be completed within 24 h of planting and the radicle begins to emerge from germinated seed within 24–48 h [41]. Oxygen is required to meet the rapid increases in seed respiration during this period. Germination cannot occur in flooded or compacted soil due to a lack of oxygen. Once the seeds have germinated, it is essential for the radicle to maintain contact with soil moisture, or the seedling may die [42]. The radicle rapidly grows downward developing into the primary root to extract moisture deep in the soil.

Both the rate of imbibition and radicle growth are dependent on temperature if water and oxygen are adequate. Low temperatures, slow imbibition, and the radicle growth rate because of high water viscosity attached to soil as well as slow seed respiratory and metabolic reactions [43]. Grain soybean germination rates range from 2 weeks or more in cold soil (10°C or less) to about 4 days under optimum soil temperatures (27–30°C) [41]. The base, optimum, and maximum temperatures of grain soybean were reported to be 4, 30, and 40°C, respectively, provided no other factors were limiting emergence [44]. It is still unknown if edamame has the same optimal germination temperatures as grain soybean. Sánchez et al. compared seedling emergence of edamame grown on 4 days/night temperature regimes (60/50, 70/60, 80/70, and 90/80°F) on 12-h cycles, and they found that 70/60°F is optimal for edamame emergence [18]. Edamame sown early may suffer from low night temperatures in the field. Mulching reportedly may help to improve the emergence of early (April) direct-seeded edamame through increasing soil temperature and reducing the variation in soil volumetric water content [45]. Moreover, soil moisture and temperature also greatly influence the activity of soil microbes, which, in turn, largely determine oxygen supply in the soil. Thus, oxygen stress may be greater in hot wet conditions [42].

Soybean seedling emergence is epigeal because the food storage organs or cotyledons are pulled above the soil surface. This is a critical step in seedling emergence, especially for edamame. Edamame has large cotyledons, which can suffer high mechanical resistance moving from below soil to above. Hypocotyls may be unable to completely pull cotyledons out of the crusted soil, resulting in a swollen hypocotyl, or even broken cotyledons, ultimately leading to seedling death before emergence is complete [46]. Other adverse field conditions, such as hypocotyl attack by insects and pathogens, can also contribute to seedling mortality in soil. Optimally, hypocotyl expansive growth can drag cotyledons upward until the arch is exposed to sunlight. Then, the arch straightens and lifts the cotyledons and growing point free of the soil surface [47]. The cotyledons unfold and begin to photosynthesize to make food for seedling growth. Finally, the cotyledons totally emerge from the soil representing the vegetative emergence (VE) stage of growth.

After the growing point and cotyledons are exposed, they become vulnerable to environmental stresses, such as hail, frost, and attacks from pests. The seedlings with necrotic lesions or physical injury to the cotyledons exhibit greatly reduced growth rates. Before the apex can be photosynthetic, cotyledons play an important role in seedling growth. Loss of one cotyledon will have little effect on yield. Loss of both cotyledons without harm to their points of attachment (*i.e.*, apical meristem), will result in 2–7% yield loss. The loss of both cotyledons, as well as their points of attachment, will result in plant death because these points of attachment will be the new growing points for the plant [47].

2.2 Seed vigor is a critical factor in germination and emergence

Successful crop establishment can be considered as a balance between environmental deterioration (such as drought, flood, soil crust, and pathogen activity) and the rate of seedling development. Both are determined by the prevailing environment, but the latter is greatly influenced by vigor [42]. Seed vigor is defined as seed ability to germinate and establish seedlings rapidly, uniformly, and robustly across diverse environmental conditions. Seed vigor measured in a laboratory is often used to predict crop establishment in the field.

Three key seed vigor traits have been identified as necessary for successful stand establishment across a wide range of seedbed conditions. The seed must—(i) germinate rapidly; (ii) have rapid initial downward growth; and (iii) have a high potential for upward shoot growth in the soil of increasing impedance [42]. All these features reduce the time between sowing and seedling emergence before the seedbed deteriorates. Although seeds from various sources germinate well under optimal conditions, they may show vastly contrasting abilities to successfully establish a crop under stressful field conditions due to variations in seed vigor.

Seed vigor is a quantitative trait influenced by the complex interaction between genetic and environmental components. It is a measure of how well seeds germinate particularly under adverse conditions. It is widely known that seed vigor can be highly variable among genotypes. Plant breeders in the US have worked decades in developing new edamame varieties with high vigor and better adaptation to the US soil and climate. On the other hand, the location of seed production, stage of maturity at harvest, seed harvesting techniques, processing, and storage conditions also affect seed vigor even in varieties with high vigor potential. In the next section, we will describe how seed vigor can be influenced by various factors including seed physiological and biochemical parameters, such as seed size, seed exudates, as well as external factors, such as temperature and humidity during storage.

2.2.1 Role of seed size on vigor

One of the biggest differences between edamame and grain soybean that may affect crop emergence is seed size. Edamame seeds are 65–100% larger than grain soybean seeds [38]. Although it is well known that the emergence of most edamame varieties is poorer than the grain type controls [34, 36], little evidence suggests that this response is due solely to large seed size. Crawford and Williams evaluated the emergence of two seed size classes (23.7 g/100-seed and 36.8 g/100-seed) within the same edamame variety. Seed size did not influence total emergence, but small seeds emerged 10% faster than large seeds [40]. This is likely due to the fact that small seeds fully hydrate faster than large ones under the same soil moisture conditions. However, more research is needed to understand the relationship between seed size and the emergence of edamame.

Although few studies on seed size in edamame have been conducted, the effect of the seed size and quality of grain soybean on crop performance has been investigated for several decades. The results are often conflicting and the literature on this topic is voluminous. Several authors have reported that small grain soybean seeds had an advantage over large seeds from the same genetic background in terms of radicle and hypocotyl development. Green et al. showed that small seed size was associated with high laboratory germination and high field emergence [48]. Edwards and Hartwig found that the small seed size (9.5 g/100 seeds) showed faster emergence and greater root development than the large seed (22 g/100 seeds) [49]. A similar finding was also reported by Kering and Zhang [39]. Hoy and Gamble found that small seed size was superior in percent emergence and speed of emergence, especially when seeds

were subjected to greater field stresses, such as low temperature and wet or crusted soils [50]. Adebisi et al. observed that for the seeds ranging from 10 to 15 g/100 seeds within the same variety, the small seed size generally produced higher seed germination and field emergence percentages, whereas large seed size produced the highest number of seeds per plant, pods per plant, and seed yield per plant [51].

There are several possible explanations for inferior germination and the emergence of large seeds in these studies. First, large seeds require more time to imbibe sufficient water to germinate, so they germinate slower compared with small seeds [40]. Second, large seeds are more sensitive to water stress, for example, the soil moisture sufficient for the emergence of small seeds may allow germination of large seeds but could be insufficient to sustain seedling growth and emergence [39]. Since large seeds require more water for normal metabolism, they are more easily damaged by reduced osmotic potential [52]. Moreover, Liu et al. stated that large seeds are more prone to oxygen deficits in the soil to support their germination [53]. Furthermore, large seeds also would likely encounter more physical resistance from soil restricting cotyledons during emergence. Seedlings developing from large seeds could be damaged during emergence in hard-crusted soils, reducing seedling vigor [42]. Finally, large seeds are prone to mechanical damage during threshing and processing prior to planting. Large seeds usually have a higher percentage of cracked seed coats, which has been reported to be negatively correlated with germination percentage [54].

However, other studies found that medium and large seeds tend to produce more vigorous seedlings and better stands than small seeds. Rezapour et al. compared germination of three seed size classes within two cultivars (*i.e.*, 13.20, 12.24, and 8.60 g/100 seeds from one cultivar and 20.16, 16.63, and 14.61 g/100 seeds from the other cultivar). The results showed that medium seeds had a higher germination percentage than those for large and small seed sizes, but no significant variations on germination rate among different seed masses were found [52]. Longer et al. reported that large seeds, in general, had a significantly greater percent emergence and greater shoot, and root fresh weight accumulation than small seeds of the same cultivar, even under stressful conditions [55]. Madanzi et al. found large seeds (19 g/100 seeds) achieved higher stand counts than small seeds (12 g/100 seeds) within the same soybean cultivar [56]. Morrison and Xue also observed that large seeds emerged better in heavier-textured soils, possibly due to the enhanced water-holding capacity which benefited large seeds, while more plants emerged from the small seeds in lighter-textured soils (such as sandy soil) [57]. Burris et al. also observed that larger soybean seeds produced larger embryos, greater cotyledonary and unifoliate leaf areas, exhibited higher respiratory rates, and possessed greater field emergence potential than small seeds. It is interesting to note that seedling emergence declined for the exceptionally large seed-sized lines (>22 g/100 seeds), presumably because of greater soil resistance to the large seed [58, 59].

It is apparent that the large seed size of grain soybean favors seedling growth. Soybean seedlings from large seeds were always larger than seedlings from small seeds [60]. Many studies have shown that the positive effects of seed size on emergence seem to be related to interplant competition [61]. Large seeds have more food storage for embryo growth and development which leads to the vigorous growth of seedlings creating competition for light and soil factors with that of small seeds, leading to higher yield [38, 62]. Finch-Savage and Bassel reported that large seeds have large cells, which have a greater capacity to grow and generate force to perform better than their smaller counterparts under stress conditions for mechanical reasons [42]. Bewley and Black also supported that large seed has abundant reserves to be planted deep in the soil where moisture is available because large seeds have a substantial store of reserves to drive seedling growth [63]. However, this is

contradictory to a recent edamame study by Crawford and Williams, who observed that edamame (large seed size) is more sensitive to planting depth and preferred to be planted in shallower depth than grain soybean (small seed size) [40].

However, it seems that the benefits of large seed on soybean emergence were observed generally for cultivars with seed mass < 20 g/100 seed [36]. In some cases, response-reactions of the small seed are similar to those of deteriorated (low vigor) seed, while in others, they are like “immature” seeds [64]. Soybean seed size is a multigenic trait that ranges in heritability from 44 to 94% [65]. While within a cultivar, maturation environment and position on the plant also affect seed mass accumulation [66]. Soybean seeds produced during drought conditions are usually smaller and less vigorous because the maternal plant’s photosynthetic capacity is reduced [67, 68]. Seeds produced in the bottom one-third of a soybean canopy were also smaller and had been reported to exhibit less forces to emerge under compacted soil conditions [69].

Finally, there are other researchers who have been unable to detect any relationship between soybean seed size and germination or field emergence [61, 70, 71]. Seed size effects seem to be less pronounced or non-existent in seeds of extremely high or extremely low vigor, or when seeds are sown under “near-ideal” environmental conditions [72, 73]. This indicates that seed quality and the seedbed environment during crop growth likely play a more dominant effect on edamame emergence than the within-cultivar seed size.

2.2.2 Seed coat

The seed coat plays a significant role in seed longevity since it protects the embryo against harmful microorganisms and unfavorable environmental conditions. The soybean seed coat is extremely hydrophilic and can absorb as much as 3.8 times its fresh weight in water [74, 75]. This water-holding capability assists the seed in avoiding imbibitional injury from the rapid hydration of dry seeds that may cause membrane damage. Abnormal seed coats can influence the rate of water uptake, increase the incidence of imbibitional chilling injury, and decrease field emergence [75]. Green et al. reported that wrinkled seed coats were more numerous in seed from earlier dates of planting and were associated with lower laboratory germination and field emergence [48]. However, Nangju found that there was no clear relation between emergence and wrinkled or discolored soybean seed. He observed that germination percentage was negatively correlated with cracked and purple-stained seed, and positively with smooth clean seed and seedling emergence [54]. Cracked seed coats also leak more electrolytes, which encourages the growth of microorganisms around seeds [76].

Seed coat thickness influences seed coat permeability which, in turn, affects the speed and probability of successful germination [77]. Thick seed coats make seeds absorb water slowly to avoid membrane damage, but an extremely hard or thick seed coat can lead to seed physical dormancy and no germination. Seed coat thickness can also be modified by environmental conditions of the mother plant and hormone treatments of the parent plant around the seeds produced [77]. For example, drought stress leads to thinner soybean seed coats, which are more permeable to water [75]. Seed-coat pigmentation is also closely associated with water uptake speed. Colored seeds usually imbibe more slowly than white-coated seeds and showed lower-level infection by *Pythium* due to less seed leakage during germination [78]. Seed coat color also helps to increase the mechanical resistance of seeds because of polymerized phenols. Soluble phenolic compounds provide a chemical defense against microorganisms [76]. Liu et al. concluded that dark-colored soybean seeds have better storability than light-colored seeds [79]. Moreover,

the expression of the impermeable seed coat trait is also influenced by seed size. The impermeable seed coat trait in soybean is of interest to researchers because impermeable seeds retain viability better than permeable seeds. Larger seeds have a higher incidence of the ruptured seed coat, which is significantly correlated ($r = -0.92^{**}$, significant at $p < 0.01$) with the impermeable seed percentage [80]. As larger seeds are more likely to exhibit a permeable response than smaller seeds, they could be more prone to chilling injury.

2.2.3 Chilling injury

Seed coat permeability has been reported to act as a principal factor in regulating imbibition rate and chilling injury. Imbibitional chilling injury is one of the key issues that reduce soybean seed quality and reduce seedling survival. Chilling injury is a physiological disorder typically associated with planting in cold soils [42, 81]. In other words, soybean chilling or imbibition damage is most severe when seeds of low initial moisture content imbibe water too quickly at low temperatures. Imbibition damage is associated with membrane dysfunction, which can reduce seed respiration, enhance the leakage of solutes, and decrease mobilization of food reserves from the cotyledons [82]. Seedlings grown from chilling damaged seeds usually show abnormalities and have less emergence force, requiring a longer period to generate maximum force [81].

As we mentioned above, seed coat color can influence seed hydration rate. Powell et al. also supported this point as they found that white-coated seed lines are more sensitive to imbibition damage than dark-coated seed lines [82]. White coated seeds imbibe quickly because they have loosely adhered testae with free space between the testae and embryo. Once the water has moved into the free space between the testa and cotyledons, embryos of white seeds imbibe rapidly. In contrast, dark-seeded lines have close-fitting testae which only allows slow water infiltration even when water can enter the seed through cracks in the testa. Moreover, cracked seeds also have a relatively high rate of water uptake, which indicates that they are more easily damaged.

Imbibition rate can be regulated by the available water around the seeds. For example, seeds priming at low osmotic potential (e.g., polyethylene glycol solutions) can minimize the effects of imbibitional damage by osmoregulation [42]. Temperature-controlled polymer coatings may also serve the same function by preventing imbibition until seeds reach a specific temperature where imbibitional damage will not occur [81]. Chilling injury easily occurs when seeds are exposed to low temperatures at the initial stages of their imbibition, thus, the critical time of chilling injury seems to be the early phase of water entry in seeds. Injury can be prevented if seeds are first allowed to imbibe only at warm temperatures [63].

2.2.4 Seed exudates

Passive release of exudates occurs as soon as seeds imbibe water and germinate [83]. These exudates are usually “normal products” of seed metabolism and they generally consist of simple sugars, such as sucrose, glucose, fructose and maltose, amino acids, flavonoids, sterols, and salts [84]. Depending on the type and abundance of microorganisms around or in the seeds, seed exudates may increase or decrease seed tolerance to abiotic and biotic stresses and affect seedling emergence. Barbour et al. observed that glutamate, aspartate, and dicarboxylic acids in soybean exudates likely represent the natural chemoattractants for *Bradyrhizobium japonicum*, a species of nitrogen-fixing bacteria that is important for nodule formation in soybean roots [85]. Martins et al. also found that malic acid in seed exudates

of common beans can promote growth and biofilm formation of the biocontrol agent *Bacillus amyloliquefaciens*, which, in turn, confers plant drought tolerance and enhances plant growth [86]. On the other side, seed exudates have also been known to promote the growth of pathogens, such as the soilborne pathogen *Pythium ultimum*, which is the causative agent of soybean seedling damping-off [87, 88].

In most cases, increased seed leakage, during imbibition, is associated with membrane damage of soybean cotyledons [89]. Aging seeds leach more electrolytes during imbibition, contributing to a reduction in seed vigor due to loss of the low molecular weight metabolites from cotyledonary cells. Hoy and Gamble reported that large seeds and low-density seeds had the highest seed leachate conductivity, which was correlated with low seed vigor [72]. Our recent study also observed that edamame seeds released exudates more quickly and showed higher seed leachate conductivity than grain soybean (unpublished results). However, specific reasons for the different rates of seed exudate production are still unknown but may be related to differential membrane leakage.

2.2.5 Seed aging

Seed deterioration during storage is one of the basic reasons for reduced seed vigor. The ability to resist aging during storage is an important physiological factor contributing to both seed viability and vigor. This is particularly problematic for soybeans as its seeds are relatively short-lived, whose longevity is only a few months [90, 91]. The longevity of soybean seeds increases progressively during seed maturation, which occurs from the phenological stage 7.2 onwards. From a developmental standpoint, this is shortly before the end of seed filling and onset of maturation drying during stage R9, corresponding to full physiological maturity [90, 92]. Several studies have reported that large soybean seeds deteriorate faster than small seeds [93]. Our recent study (unpublished data) also supports reduced storage life, since we found that edamame seeds aged faster than grain soybean seed when stored under the same conditions.

The longevity of seeds in storage is influenced by four major factors, (i) genetics, (ii) maturity and quality of the seed at the time of harvest and storage, (iii) moisture content of seed or ambient relative humidity, and (iv) temperature of storage environment [93]. Soybean seed vigor declines rapidly with increasing storage duration, but the severity of reduction varies by genotypes. Heatherly et al. reported that the germination of grain soybean declined from 96 to 12% and 93 to 21% in two cultivars after 20 months of seed storage, while for another cultivar, it only declined from 98 to 75% [94]. Temperature and seed moisture content are the two main environmental factors affecting seed storage longevity. Nkang and Umoh compared soybean germinability after 6 months of storage under storage temperatures 0, 25, 35, 45, and 55°C and relative humidities of 45, 55, 65, 75, and 84%. They reported that optimum storage occurred at temperatures of 25–30°C and relative humidity of 55–65% [95]. Mbofung et al. evaluated germination of soybean seeds stored under 10°C; 25°C; in open storage in a warehouse at ambient humidity. High seed viability was maintained for seeds stored at 10°C (>92%) and moderate in the 25°C (>78%) after 20 months, with almost 0% germination for the seeds stored after 20 months at a warehouse [96].

The hydrophilic nature of the high protein content of soybean seed drives the absorption of water from the environment during imbibition, increasing hydrolytic enzyme activity and increasing seed respiration [93]. Seed deterioration is thought to be due to lipid peroxidation, leading to mitochondrial dysfunction, and less ATP production in seeds [97]. High temperatures and seed moisture accelerate the rate of biochemical processes, causing more rapid seed deterioration resulting in first

reduced vigor and eventually seed death. Moreover, high temperature and seed moisture can also stimulate the growth of storage fungi on seeds that rapidly reducing seed quality.

In addition, the rate of seed deterioration during storage is also affected by packaging materials. Since soybean seeds without hard seed coats are hygroscopic, they will take up moisture from the atmosphere when in open storage. This means that when the relative humidity is high, seed moisture content increases, and when the humidity is low seeds can lose water to the atmosphere. In humid areas to maximize storage life, it is recommended to dry seeds to moisture contents below 14%, the threshold for microbial growth, and store seeds in sealed packaging with a moisture barrier; so, there is no increase in seed moisture during storage. Several studies show that containers with moisture barriers improve the storage life of soybean seeds. Polythene bags are superior to cloth bags because they keep moisture out during seed storage [98]. It is reported that the storability of soybean cultivars could be enhanced by 4 months when storing dried seed in polythene bags compared to cloth bags [99]. Monira et al. reported that cloth bags are not safe for long-term soybean seed storage compared to polyethylene bags or metal containers, since the rate of moisture absorbance was higher in cloth bags with no moisture barrier [100]. They also reported higher fungi growth in cloth bag seed storage and metal containers than in polythene bags. Fungal growth in sealed storage occurs when the seed moisture content is too high at the time of packaging. Others have reported that soybean seeds stored in aluminum foil bags have higher germination followed by polyethylene and wheat bags when stored for the same period of time at the same temperature [101].

Moreover, the storability of soybean seeds is also influenced by many pre- and during-harvest factors, including climate conditions during seed production, pest attacks on seeds and pods, disease infection on developing and maturing seeds, premature or delayed harvest, and how the seeds are harvested and processed [54, 102]. Delayed harvest and intense rainfall during pod maturation can increase seed deterioration during storage. A previous study reported that a delay in the harvest of about 2–4 weeks after optimum maturity reduced seed quality [54].

2.2.6 Seed maturity, harvest, seed shape

Maturity groups are thought to have no influence on seed vigor [96]. However, early maturing soybean plants developing during hot, dry conditions increased the number of seeds with morphological defects. These defective seeds germinated and emerged later than seeds maturing on soybean plants that developed after the hot, dry weather conditions were over [103]. For example, the combined occurrence of heat (air temperature above 30°C) and drought stresses during seed filling can increase the percentage of shriveled soybean seeds; a higher incidence of shriveled seeds was observed on the upper third of the mother plant [104]. Germination and emergence were significantly reduced as the level of shriveling increased [104]. Severe other stresses (such as defoliation) during seed filling can also produce small, flat, shriveled, and underdeveloped seeds with poor germinability and vigor [105]. Moreover, the vigor of normal-looking soybean seeds (not wrinkled or shriveled) formed at high temperatures was reduced in comparison to seeds formed at optimal temperatures [106].

2.2.7 Seed mechanical damage

Mechanical injury is another cause of significantly reduced seed vigor. Soybean seed is very susceptible to mechanical damage since the vital tissues of the embryo (radicle, hypocotyl, and cotyledon) lie under a thin seed coat that offers little

protection [107]. In most cases, the damage may not be sufficient to kill seeds but may cause abnormalities in seedlings or cracks in the seed coats, reducing seedling establishment [107]. Mechanical threshing is one of the processes where seed damage occurs because of the abrasions and impacts when seeds pass through a combine [108]. It is reported that large-sized seed is more prone to mechanical damage during harvesting and processing, as cracked seed coats are more common in large soybean seeds [54]. Harvesting seeds at high moisture content can be used to reduce mechanical damage which is greater when seed moisture contents are extremely low.

2.3 Other environmental factors related to the emergence

The soil seedbed is a complex environment in which seeds and seedlings are exposed to multiple stresses. As discussed previously, soil temperature, oxygen, and water content (Section 2.1) play a critical role in seed germination, seedling vigor, and successful establishment (Section 2.2). In the following section, we discuss the effects of some other environmental factors, including the abiotic factors (soil compaction and the planting depth) and the biotic factors (soil microorganisms and insects) on stand establishment. Biotic and abiotic effects on stand establishment can have a pronounced effect on establishment especially when the seeds are of suboptimal quality.

2.3.1 Soil strength

In addition to soil temperature, moisture, and oxygen availability mentioned above, soil strength, another edaphic factor often the result of crust formation at the surface of soils with high clay content, also plays a key role in pre-emergence seedling growth since the hypocotyl may encounter considerable resistance when pulling the cotyledons through crusted soil. If the cotyledons face more mechanical impedance from the soil than the force exerted by the hypocotyl, the hypocotyl may collapse between the cotyledons, producing an abnormal seedling. Even worse, the hypocotyl may break, resulting in seedling mortality [46].

Soil crusting is likely to occur on high clay content soils when the surface dries rapidly following a heavy rainfall [109]. The hard layers at the soil surface show low permeability and high tensile strength making seedling emergence difficult. Another soil structure problem is compaction, which occurs when soil particles are pressed together, reducing pore space between them and consequently increasing the bulk density [110]. Soil compaction is usually caused by compressive forces applied from wheels of heavy field machinery (such as tractors, trucks, and combines) and pressure from the hooves of livestock or other animals [111]. Increased soil bulk density can reduce root growth as well. Severe compaction can also decrease a soil's permeability to water and air. This decrease in permeability will reduce the activity of soil microorganisms and the rate of organic matter decomposition thus slowing the release of essential mineral nutrients needed for seedling growth. These soil problems can be eliminated by using a rotary hoe mounted on a tractor or other similar equipment.

Soil strength is not likely to affect seed germination [42], instead, the increasing soil strength caused by compaction of heavy soils can impair root elongation, particularly on shoot development of pre-emergent seedlings in severely crusted soils [112, 113]. Seedling response to soil strength is associated with seed vigor. Hyatt et al. reported that soybean emergence declined as compaction increased from low ($4.6 \text{ kJ m}^{-3} \text{ CE}$) to high ($22.9 \text{ kJ m}^{-3} \text{ CE}$); however, the emergence of high-vigor seed lots remained $>80\%$ until compaction increased to $13.7 \text{ kJ m}^{-3} \text{ CE}$, while low-vigor seed lots had low emergence ($<50\%$) even at the

lowest compaction ($4.6 \text{ kJ m}^{-3} \text{ CE}$) level [114]. The authors also observed that seed size had no effect on emergence at any level of compaction. However, other studies claimed that larger soybean seeds should be subjected to greater mechanical resistance due to their large cotyledons [40, 59]. Soil strength is closely related to the capillary pressure of water in the pores holding the soil particles together. Clay soils tend to have a higher degree of saturation (thus greater capillary pressure) resulting in higher soil strength than sandy soils [42]. In an ideal situation, the soil structure will minimize water loss by evaporation while remaining mechanically weak with no barrier to growth [42].

2.3.2 Plant depth

Planting depth is an essential management decision influencing emergence of soybean seeds. Depth is correlated to total, rate, and uniformity of emergence. Deep depth causes delayed emergence which may increase seedling mortality by extending the window of time in which seedlings are vulnerable to soil pathogens, risk of soil-crusting, and anaerobic soil conditions [40]. While shallow planting can also be detrimental to emergence when the upper soil lacks sufficient moisture for seed germination and seedling establishment.

Recommended planting depth of grain-type soybean has been reported to be 2.5–5 cm [40, 46, 115], specifically depending upon the soil type and weather conditions (such as rainfall and temperature). In sandy soils, seeds can be planted deeper, while in heavy clay soil, seeds should be planted shallower [46]. Fehr et al. reported a reduction of an average emergence of 73% from 5 cm to 44% from 10 cm among different grain soybean varieties [116]. Varieties also showed variations in response to deeper planting depth, as the emergence of some cultivars was reduced markedly (as low as 13%) at a depth of 10-cm depth [116], partly due to lower seed vigor.

The optimal planting depth for edamame is unresolved, although a few studies have attempted to address it. Zhang et al. found the hypocotyl and radicle of edamame were significantly longer and wider than that of the grain soybean. As planting depth increased from shallow (1 cm) to deep (5 cm), emergence declined for both grain soybean and edamame in a growth chamber, but the grain soybean seed consistently emerged better than the vegetable soybean seeds. The emergence of both the grain soybean seed and the vegetable soybean was >65% until planting depth increased to 3 cm, while the vegetable soybean seed had the lowest emergence (<30%) at the deepest (5 cm) level. Thus, the vegetable soybean was relatively more susceptible to planting depth than the grain soybean, and 3 cm planting depth was an acceptable depth for both types of soybeans [46]. Crawford and Williams also reported similar findings under field conditions. They compared the emergence of edamame and grain soybeans at depths of 1, 2, 3, and 5 cm in the field, and they found that edamame emerged more completely and quicker at the shallowest depths examined if sufficient soil moisture was available [40]. Other studies recommended a planting depth for edamame seeds not greater than one-half inch deep to avoid reduced emergence [117, 118]. All of these results show that if moisture is adequate in soil, the optimal planting depth of edamame should be shallower than grain-type soybean. However, it is hard to conclude what the optimal depth for edamame should be because of variation among varieties, soil, and weather conditions. Under the drought condition, edamame may need to be planted deeper to access soil water reserves [56]. However, the larger edamame seed size may inhibit emergence, particularly in heavy soils prone to compaction and crusting at deeper depths, reducing emergence, especially with suboptimal seed quality.

2.3.3 Seed and seedling diseases caused by soilborne pathogens

Similar to grain soybean, seed and seedling diseases, caused by soilborne fungal and oomycete pathogens, such as *Fusarium* species, *Phytophthora sojae*, *Pythium* species, and *Rhizoctonia solani*, are also common causes of decreased edamame stands and may cause serious or even complete yield loss [36, 119, 120]. These pathogens can survive in the soil for many years, and they can kill seeds (seed rot) or cause seedling death shortly after emergence (damping-off). The higher sugar content and size of edamame seeds mean that they leach more nutrients into the soil upon imbibition compared to smaller grain soybeans. This leachate feeds and attracts microbial pathogens leading to greater seedling mortality [42, 121]. Fungicides (either as an in-furrow or as a seed treatment) with broad-spectrum fungicides provide the most reliable approach to protect against soilborne pathogens. Recently, it is reported that edamame seedling emergence can be improved using seed treatment with fludioxonil + mefenoxam [36]. However, other studies pointed out that fungicides should be used only when the seeds or soil are contaminated with pathogens [75], otherwise biological N₂ fixation may be severely affected due to the toxicity of most fungicides to bradyrhizobia [122, 123]. In addition, no fungicide seed treatment can consistently improve field emergence of seeds with reduced quality for reasons other than a disease, such as mechanical damage, age, or size [124].

With rising public awareness of the potential environmental and health hazards of agrochemicals, the demand for organic edamame has been increasing and constitutes a large portion of the market. Thus, researchers are charged to search for alternatives to fungicides to improve edamame seedling emergence. Biological seed treatments are playing a pivotal role in sustainable crop production by providing a combination of both effective performance and product safety. In general, biological control agents contain natural active ingredients that can include microbes, such as bacteria and fungi, plant or algae extracts, as well as other organic substances. Previous studies have shown some fungal or bacterial strains, including *Trichoderma harzianum*, *Streptomyces* sp., *Bacillus subtilis*, and *Pseudomonas putida* are used or may be potentially effective as biological seed treatments for grain soybean to control soilborne diseases and improve seedling establishment [125–127]. However, there are still no studies examining the effectiveness of biological seed treatments for improving emergence or crop safety when applied to edamame.

A few studies have also focused on evaluating the disease resistance of different varieties of edamame [128–130]. High susceptibility to *Phytophthora* spp. causing root rot disease was found in cultivars “C784” and “Bunya” in Australia. Different degrees of resistance to *Diaporthe phaseolorum* causing soybean seed decay and stem canker were observed in edamame varieties in Argentina. However, more work still needs to be done to test current commercial edamame cultivars for resistance against more soilborne diseases to assist in developing more disease-resistant cultivars.

2.3.4 Insect pests

There are several insect pests that can attack edamame, but most of them eat the foliage of emerging plants or only affect the pod quality without significantly reducing yield [131]. These pests include various beetles (such as Mexican bean beetle, Japanese beetle, bean leaf beetle, and cucumber beetle), grasshoppers, leafhoppers, thrips, loopers, other worms (such as green cloverworms and defoliating caterpillars), and stink bugs. Only some early-season insect pests, such as

wireworms, seedcorn maggots, and white grubs can damage soybean seeds and seedlings [132]. For example, soybean seeds or cotyledons may be attacked by seedcorn maggots when cool, moist conditions prevail, and germination and early growth are slowed. Generally, insecticide seed treatments and hand picking are enough to achieve control [117].

Other animals, such as slugs, rabbits, birds, and deer can do extensive damage to young seedlings [118]. Deer love edamame leaves, and cotyledons, and can quickly defoliate plants. Repellants, scare devices, and fencing can provide temporary protection [133].

3. Conclusion

This chapter has attempted to define the seed intrinsic and environmental factors associated with edamame germination and seedling establishment. It provides readers with a knowledge of the aspects of environmental influence on seed quality and its subsequent effect on seedling emergence, which can be helpful for a comprehensive understanding of the causes of poor edamame seedling emergence that some farmers now face. It should be emphasized that seed quality still plays a critical role in edamame emergence. There is a high potential for edamame seeds with strong viability and vigor to exhibit excellent emergence (>80%). On the other hand, however, the large seed size of edamame contributes to the emergence problem. First, large seeds are more sensitive to poor seedbed environments, including inadequate soil moisture, improper temperature, and soil obstruction. Second, large seeds are more prone to reduce viability and vigor because of mechanical damage during seed harvest, processing, and are also more likely to age during storage. Third, large seeds leach more nutrition during imbibition, thus attracting soilborne pathogens and increasing disease occurrence. All of these contribute to the lower emergence ability of edamame in the field when compared with that of grain-type soybean seeds.

4. Future perspectives

When the causes of emergence problems are understood, the corresponding strategies could be made to enhance edamame seed performance and establishment. Developing edamame cultivars with high seed vigor and better adaption to the US soil and climate, as well as optimizing the conditions of seed processing and storage will be a goal for plant breeders and seed industries to improve seed quality and edamame emergence. Proper planting (such as optimal planting depth) and field management (such as seedbed preparation, *i.e.*, the soil is warm, moist but well-drained, fertile, and free of weeds) are also critical to ensure robust seeding growth in the field. Since only a few edamame production practices were described in this review, due to the limited research that has been conducted, more research focusing on edamame is needed to develop the appropriate management practices for edamame production. This will ultimately support a more reliable edamame supply into the future.

Conflict of interest

The authors declare no conflict of interest.

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