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Soybean Seed Production and Canopy Photosynthesis in Cultivation

Kiyoshi Nagasuga

Abstract

The mechanism of soybean seed production is very complicated. Soybean yield is strongly associated with pod number and seed number; these are prompted by light interception and growth during the period between beginning blooming and beginning seed. But vigorous shoot growth during the vegetative stage does not contribute to pod growth and harvesting. In humid regions of Asia, soybean cultivation is incorporated into the rotation cropping in converted paddy fields, and wet soil often causes poor germination. Soybean leaves, trifoliolate wide flat leaves, are easy to concentrate to the upper layer of the canopy. This suppresses light penetration to the lower layer and, as a result, produces imperfect seed yield in spite of enough biomass. Daytime leaf movement is useful for light penetration and photoinhibition in leaf photosynthesis. Leaf photosynthesis is generally associated with high yield; however, the relationship between them is not clear. It is necessary for high soybean yield not only to elucidate the mechanisms that these factors suppress soybean seed production more clearly but also to select the cultivars and cultivation suitable for the climate in each area.

Keywords: biomass, canopy photosynthesis, cultivation, germination, light interception, lodging, pod, seed production

1. Introduction

Soybean is one of the important crops for oil and protein resources. Soybean production in 2016 is 336 million tons, and about 80% of the world production depends on a few major producers, the United States, Brazil and Argentina [1]. World soybean production continuously increases at a remarkable rate for the last several decades; it reached ca. 265 million tons in 2010 from ca. 30 million tons in 1970 [2]. This increase is associated with the improvement of soybean production; yield gain of the United States is 22.6 kg/ha/year from 1924 to 1997 and 12.1 kg/ha/year from 1950 to 1991 in China [3]. High soybean yield is also an important agricultural strategy not only in the major producers but also in the minor producers such as India, Japan and other Asian countries. Many researches about soybean production were actively made to achieve high yielding; for example, more than 60 years of researches have produced various types of soybean cultivars in Japan because soybean is the fundamental material of Japanese foods. However, these trials cannot find the breakthrough that improves soybean production in this country; Japanese

soybean yield (160 kg/10a) has been steady values for the current decade [4]. World soybean production polarized.

Improvements in weed control and planting and harvest machinery as well as the incorporation of disease and lodging resistance into elite soybean germplasm have contributed to the yield improvement in continental North America [5]. In addition, many theories on the physiological traits associated with genetic yield improvement have been put forward; however, there are still some incongruencies among these theories [6–9]. Therefore, it is important for soybean yield improvement to understand the relationship between yield and quantitative physiological traits.

2. Seed yield and biomass

In general, the yield of crop plants can be expressed as the function of biomass and harvest index as follows:

$$\text{Yield} = \text{Biomass} \times \text{Harvest index}$$

Biomass is the total amount of living organisms in a given area. Biomass contains leaf, stem, root and seed (full maturity). Harvest index is harvested product (seed) as a percentage of total crop weight. Although high biomass does not always result in high yield, low biomass cannot result in high yield even if crop plants could realize remarkable high harvest index. So the increase in biomass is easier to result in high yield than that of harvest index. Meanwhile, the improvements of crop yield by breeding are also associated with the increase in harvest index, for example, 1.50 times increase in Chinese rice yield is attributed to 1.16 times that of biomass and 1.33 times that of harvest index by breeding [10]. It is depending on the crop species whether a numerous increase of crop yield is attributed to the increases in biomass, harvest index or both.

In soybean, harvest index is often regarded as seed/stem ratio, not seed/shoot ratio because soybean leaves start to get yellow around beginning maturity and have been shedded at full maturity. The reports on the role of harvest index on soybean seed yield include both significant [8] and no significant [6, 11–13] correlations with harvest index. However, even the researchers who reported significant correlation between yield and harvest index suggested that the increase in harvest index contributed little to increased yield potential of modern genotypes [9, 14]. It seems that harvest index is not an important contributor to genetic yield improvement; the increase in biomass is more useful for high yield of soybean plants.

Breeding often improves crop yield through the increase in biomass. Plant biomass is composed of 70–90% water and 10–30% dry matter [15]. Water is a very important material for life; this controls life maintenance and plant growth strongly. However, it is necessary for a large increase in plant biomass to get not only abundant water but also much dry matter. Dry matter is derived from CO₂ fixed through photosynthesis [16, 17]. Photosynthesis produces the basic carbohydrates used for producing more complex carbohydrates, proteins and lipids, all of which contribute to dry matter [18]. Dry matter weight is a more reliable measure of mass than fresh weight (biomass) because dry matter excludes the fluctuating water concentrations [19] so the effect of soybean biomass on yield is evaluated through that of total dry matter weight in this study.

Before the correlation between yield and total dry matter weight is mentioned, descriptions of growth stage of soybean during the growing season according to Fehr and Caviness (**Table 1**; [20]) and its relationship with growth parameters

Stage	Descriptions	
Vegetative stage		
VE	Emergence	Cotyledons above the soil surface
CV	Cotyledon	Cotyledons and unifoliates are fully expanded
V1	First node	One unrolled trifoliolate (leaflets do not touch) on the main stem
V2	Second node	Two unrolled trifoliolate (leaflets do not touch) on the main stem
V(n)	Nth node	N unrolled trifoliolates (leaflets do not touch) on the main stem
Reproductive stage		
R1	Beginning bloom	One flower at any node on the main stem
R2	Full bloom	One flower at one of the two uppermost nodes on the main stem with a fully expanded trifoliolate
R3	Beginning pod	A 0.5-cm-long pod at one of the four uppermost nodes on the main stem with a fully expanded trifoliolate
R4	Full pod	A 2-cm-long pod at one of the four uppermost nodes on the main stem with a fully expanded trifoliolate
R5	Beginning seed	Seed is 0.3 cm long in a pod at one of the four uppermost nodes on the main stem with a fully expanded trifoliolate
R6	Full seed	A pod containing a green seed that fills the pod cavity at one of the four uppermost nodes on the main stem with a fully expanded trifoliolate
R7	Beginning maturity	One pod anywhere on the main stem with the mature brown color
R8	Full maturity	95% of pods reached mature color

Table 1.
 Descriptions of growth stage of Soybean [20].

including total dry matter weight are mentioned. Although soybean leaf is trifoliolate, the cotyledon pulled by the hypocotyl emerges out of the soil (germination, VE), and the first leaves are two unifoliates (cotyledon, VC).

Infection of *Bradyrhizobium japonicum* and nodule formation start around the second node (V2). Plant length and leaf area index increase gradually after emergence and reach more than 80% maximum values around beginning bloom (R1). Canopy structure is also almost achieved around this period. On the other hand, total dry matter weight increases slowly from emergence to R1 and then exponentially until beginning pod (R3). The maximum values are reached at beginning seed (R5) or just before full seed (R6), and then total dry matter weight decreases by maturing. However, some cultivars with vigorous vegetative growth capacity sometimes increase total dry matter weight continuously around beginning maturity (**Figure 1A**) [21]. Soybean development is separated into vegetative period (emergence to R1) and reproductive period (R1–R7). However, vegetative growth (leaves, stems and nodes) extends from emergence to R5. The reproductive period is separated into flowering/pod formation period (R1–R6) and seed filling period (R5–R7). Pod and seed numbers are determined until R6 [22].

There is a hypothesis that soybean yield is limited by the activity of the source (i.e. canopy photosynthesis) [23]. One of the reasons is low ratio (19–64%) of pod set (from flower to pod) in soybean plants [24–26]; many flowers fall not only by environmental stress (i.e. low temperature [27], water shortage [28] and light energy shortage [29]) but also by nutrient competition between flowers in the plant

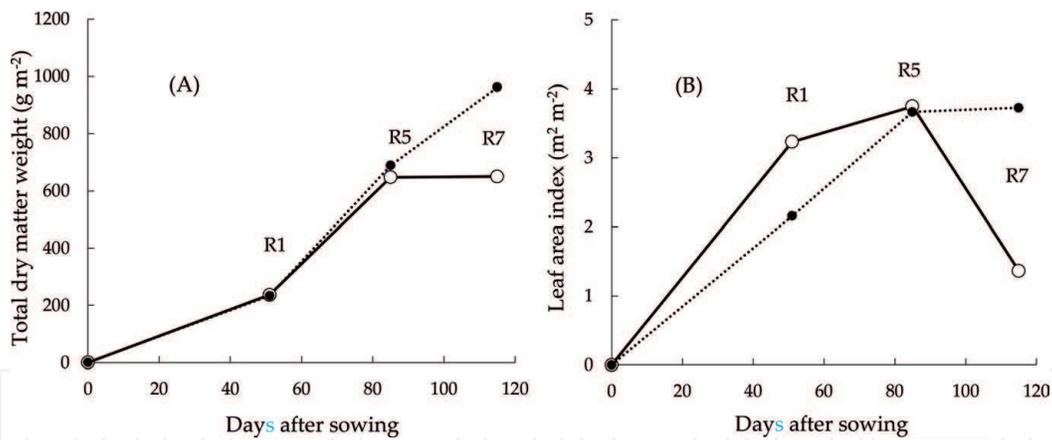


Figure 1.

Changes in total dry matter weight (A) and leaf area index (B) in Fukuyutaka (open) and Misato-zairai (close). Fukuyutaka and Misato-zairai are the maturity group II determinate genotypes. Fukuyutaka, cultivated variety, has relatively staple seed yield; however Misato-zairai, local cultivar, has an unstable one [21].

or with vegetative organs [30]. Above-ground (particularly leaves) of crop plants is main photosynthetic organs and this increase is associated strongly with nitrogen content in the soil [31]. Basal fertilizer is generally applied to promote vigorous photosynthesis and crop growth from early growth stage. However, total dry matter weight before flowering has little effect on seed yield in soybean plants [32]. In addition, the reports on the association between biomass and seed yield have presented conflicting results; some researchers reported that total dry matter weight was not significantly related to yield improvement in 14 short-season soybean cultivars from different eras of release [8, 33, 34]. On the other hand, after the onset of reproductive development, many researchers indicate a positive association between dry matter accumulation and seed yield [9, 14, 35–37]. There are also conflict reports about more critical period after flowering, some reports described the period between R1 and R5 [36, 38, 39], and others are after R5 [35, 40]. However, seed weight is often associated with seed number and pod number strongly, and seed number depends on pod number. **Figure 2** shows variation in seed weight as a function of pod number (A), seed number (B) and the relationship between seed

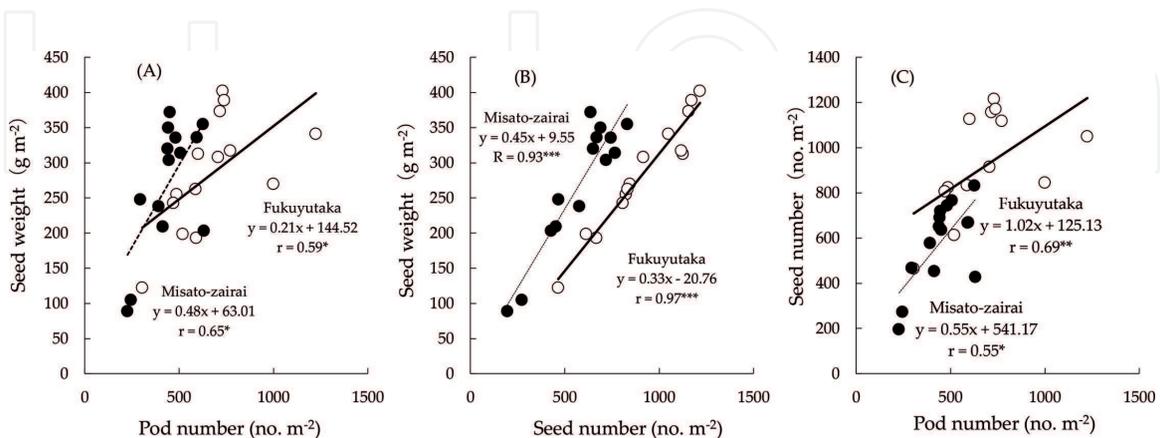


Figure 2.

Variation in seed weight as a function of pod number (A), seed number (B) and the relationship between seed number and pod number (C) at maturity (R8) in Fukuyutaka (open) and Misato-zairai (close) cultivated at Mie Prefecture in Japan in 7 years (unpublished data). Experimental field, plant density, fertilization and the measurement of yield components in these experiments were the same as the previous studies [21, 41–44]. Main data are those of normal sowing (early-middle July sowing at Mie) from 2008 to 2014 (excluding 2012) [21, 41–44], and the same include early sowing (middle May and middle June in 2009) and irrigation treatment (from blooming in 2009 and from 1 month after sowing in 2013 and 2014) [43, 44]. r is correlation coefficient. *, **, ***: significant at 0.5, 0.1 and 0.01%, respectively.

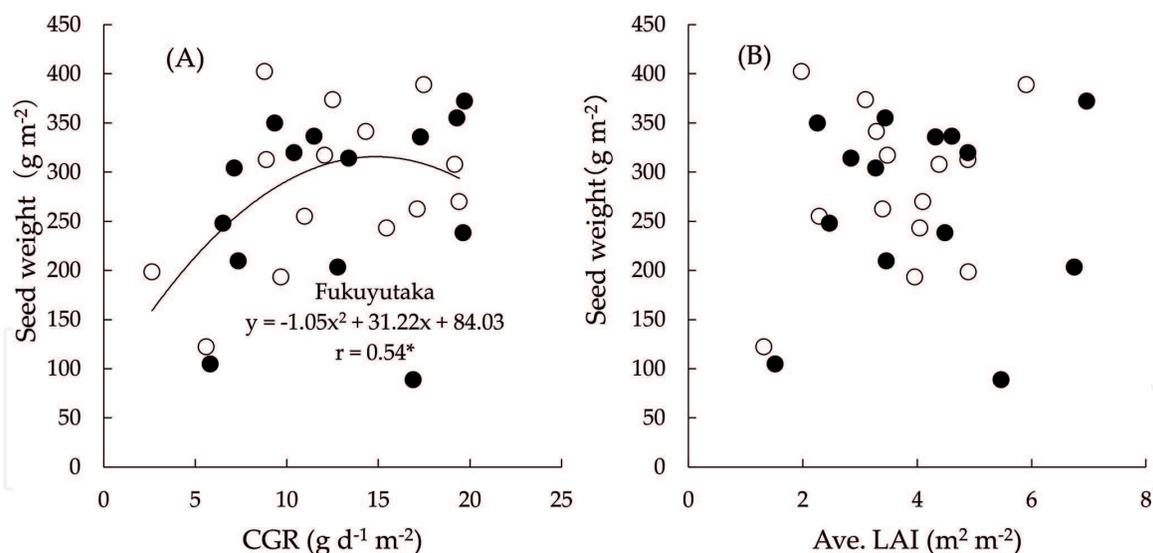


Figure 3. Variation in seed weight at maturity (R8) as a function of crop growth rate (CGR, A) and average leaf area index (Ave. LAI, B) from beginning bloom (R1) to beginning seed (R5) in Fukuyutaka (open) and Misato-zairai (close) cultivated at Mie Prefecture in Japan in 7 years (2008–2014, unpublished data). The samples are the same as those in Figure 2, and CGR and ave. LAI were measured according to the previous studies [21, 41, 43]. *r* is correlation coefficient. *: significant at 0.5%.

number and pod number (C) at maturity (R8) in Fukuyutaka and Misato-zairai cultivated at Mie Prefecture in Japan in 7 years (2008–2014). Misato-zairai has larger seed size and lower seed number than Fukuyutaka; however, the relationships among seed weight, seed number and pod number are similar in these cultivars. Pod formation is nearly completed by R3 [39]. Although there are no positive relationships between seed weight and total dry matter weight at R5, crop growth rate (CGR, dry matter accumulation per day) during the period between R1 and R5 is easy to be associated with seed weight (Figure 3). The period between R1 and R5 is considered critical for the impact of assimilatory capacity on yield, and it would be necessary for high soybean yield to make active photosynthetic performance.

On the other hand, the initial growth often has a serious impact on seed yield in the monsoonal area of Asia. Soybean often cultivated in the converted paddy fields and excessive rainfall and poor drainage frequently depending on rotation cropping often cause waterlogging in this area. Soybean is vulnerable to waterlogging, which threatens soybean productivity [2]. The most sensitive growth stage is around emergence, particularly germination. Poor emergence has a serious impact on soybean production because this decreases plant density radically. Waterlogging suppresses soybean seed germination through the several manners. Firstly, waterlogging destroys seed tissue by abrupt cell expansion because soybean seeds absorb water rapidly in this condition [45, 46]. Secondly, waterlogging inhibits the respiratory activity of germinating seeds. Germination is an integrated process consisting of many metabolic events; therefore, active respiration is necessary for its metabolism and germination. Excessive soil moisture condition decreases oxygen concentration in the soil and inhibits seed respiration. Thirdly, soybean seeds in the waterlogging condition are vulnerable to soil-borne diseases, which often results in seed corruption and the inhibition of seed germination. On the other hand, waterlogging also suppresses soybean emergence physically. Waterlogging or hard rain destroys the crumb structure of culture soils, which makes soil surface hard like a plate. These suppress emergence through the blockage of hypocotyl extension even if seed germination succeeds. After emergence, waterlogging also threatens soybean productivity through the suppression of root respiration, growth and symbiotic nitrogen fixation by root nodules and the spread of soil disease infection. These have a great impact

on vegetative growth, which inhibits pod number per plant, seed number per pod and seed weight. Meanwhile, the emergence is strongly correlated to plant density and hill number per area; suppression of emergence by waterlogging often decreases plant density dramatically. Because of insufficient shoot dry matter weight and leaf area per unit area, low plant density is difficult to result in high yield in various crop plants [47–49]. Therefore, low plant density by waterlogging has a serious impact on soybean yield. The cultural or genetic improvements of soybean emergence are more important in the monsoonal area of Asia.

3. Canopy photosynthesis and its related parameters

After emergence, active photosynthetic performance of canopy is useful for high seed production of soybean plants. Canopy photosynthesis can be composed of three parameters: leaf area index, light intercepting efficiency and photosynthetic rate per unit leaf area (leaf photosynthesis).

3.1 Leaf area index

Leaf area index means total leaf area per unit ground area [50]. Leaf area index can be expressed as the product of plant density and total leaf area of a plant. Plant density is a factor that is easy to control by cultivation: dense planting increased leaf area index through the increases in plant density easily and quickly. However, crop shoots in high plant density are spindly and often result in lodging [47–49]. So it is necessary for the increase in leaf area index both to keep optimum plant density and to increase leaves with the capacity of leaf appearance and expansion of crop plants itself.

Soybean leaves develop acropetally from individual nodal primordia on the main stem as well as on the branches. The rate of individual leaf appearance, expansion and duration as well as its interaction with environmental factors has an impact on leaf area index development. Each leaf unrolls, expands and persists in the expanded state for a period of time prior to senescence and finally abscission. **Figure 1B** shows change in leaf area index in Fukuyutaka and Misato-zairai. Typical changes in soybean leaf area index are that of Fukuyutaka: leaf area index increases dramatically during vegetative period, and maximum value is achieved by around R5. After that, leaf area index begins to decline and this decline accelerates by leaf abscission before R7. Leaf area index has an impact on canopy ability to intercept solar radiation and light interception up to 95% of incident solar radiation around R5 [5]. In this stage, canopy closure is observed and this corresponds to leaf area index of 3–5 [33]. A leaf area index greater than 5 can be sometimes observed; however, this is not easy to result in the increase in radiation interception any further [51].

High crop growth rate is usually associated with high leaf area index in crop plants [31]. Soybean leaf area controls strongly crop growth rate during the vegetative period, and the increase in total leaf area is associated with node number of main stem and specific leaf area (leaf area/leaf dry matter weight) [52]. Leaf growth is often associated with environmental factors (i.e. water, temperature, nitrogen, light intensity). During the vegetative period, leaf area increases with sufficient soil water, and severe soil drought restricts strictly leaf growth in the high air temperature condition; however, low air temperature condition negates the effect of soil water condition on leaf growth, and the difference in total leaf area between wet drought soil conditions is too small in Japanese soybean cultivar (**Figure 4**) [53].

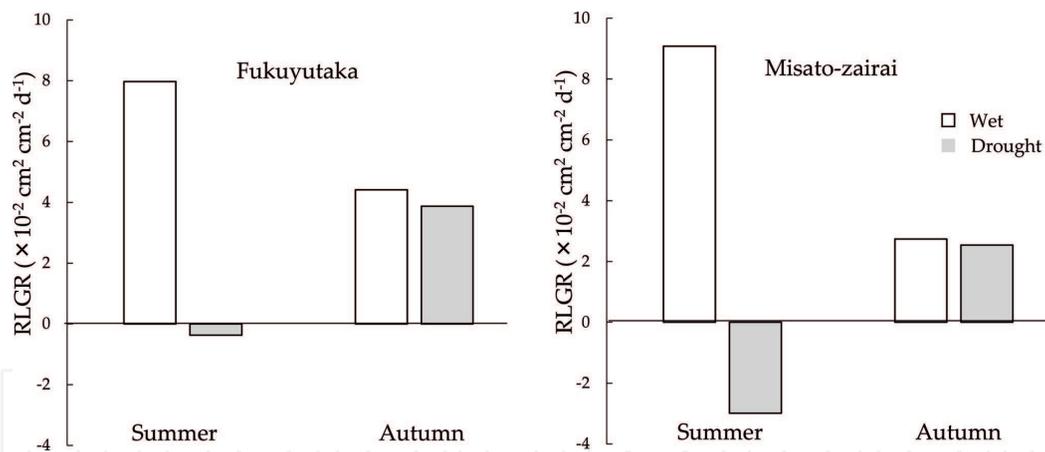


Figure 4. Relative leaf growth rate (RLGR) of Fukuyutaka and Misato-zairai grown in wet and drought soil conditions during the vegetative stage in summer and autumn. After 1 month of cultivation, supply of water to some plants was suppressed for 2 weeks (drought). Relative growth rate is daily leaf area accumulation per leaf area [53].

There is an optimum leaf area index where crop growth rate reaches the maximum level. Crop growth rate increases with increment of leaf area index, attains the maximum level and then decreases with increase of leaf area index. In soybean plants, the increase in leaf area index is easy to result in that of crop growth rate during R1–R5 [41], and this is associated with higher specific leaf area, not leaf weight ratio (leaf dry matter weight/total dry matter weight) [41]. However, higher leaf area index has a negative impact on seed yield. There is a weak relationship between average leaf area index during the period between R1 and R5 and seed weight at R8 in Fukuyutaka and Misato-zairai (**Figure 3**). Higher leaf area index would be useful for high biomass, but not for seed production in soybean plants.

3.2 Light intercepting efficiency

Light extinction coefficient can be used to quantify the extent of light penetration into the plant canopy of various species. The light extinction within the canopy follows Lambert-Beer's law [31]:

$$\ln I/I_0 = -kL$$

where I_0 is the incident light intensity on the canopy and I is the light intensity at a certain level in the canopy where the cumulative leaf area index from the top of the canopy is L . The value of k is the light extinction coefficient which is specific to the respective plant canopy. The decrease in the extinction coefficient represents an increase in light penetration into the plant canopy. A monocotyledonous plant (i.e. rice) showed a small value of k . The meristem of rice plant locates at the junction between the stem (leaf sheath) and root during the vegetative stage [54]. Although the meristem rises with making anthesis, much nodal primordia with long, thin and upright leaves still concentrate to the lower layer [54]. So, leaves are distributed widely from the lower to upper layer of the canopy (**Figure 5A**). On the other hand, a dicotyledonous plant with round leaves (i.e. soybean) showed larger k . The meristem of dicotyledonous plant locates at the shoot apex, and this rises continuously (or until flowering in determinate genotypes) [55]. Therefore, the nodal primordia locate at various layers of the canopy. In addition, the leaves expand from the apex of petiole. These result in the concentration of each leaf over the middle layer of the canopy (**Figure 5B**, [21]).

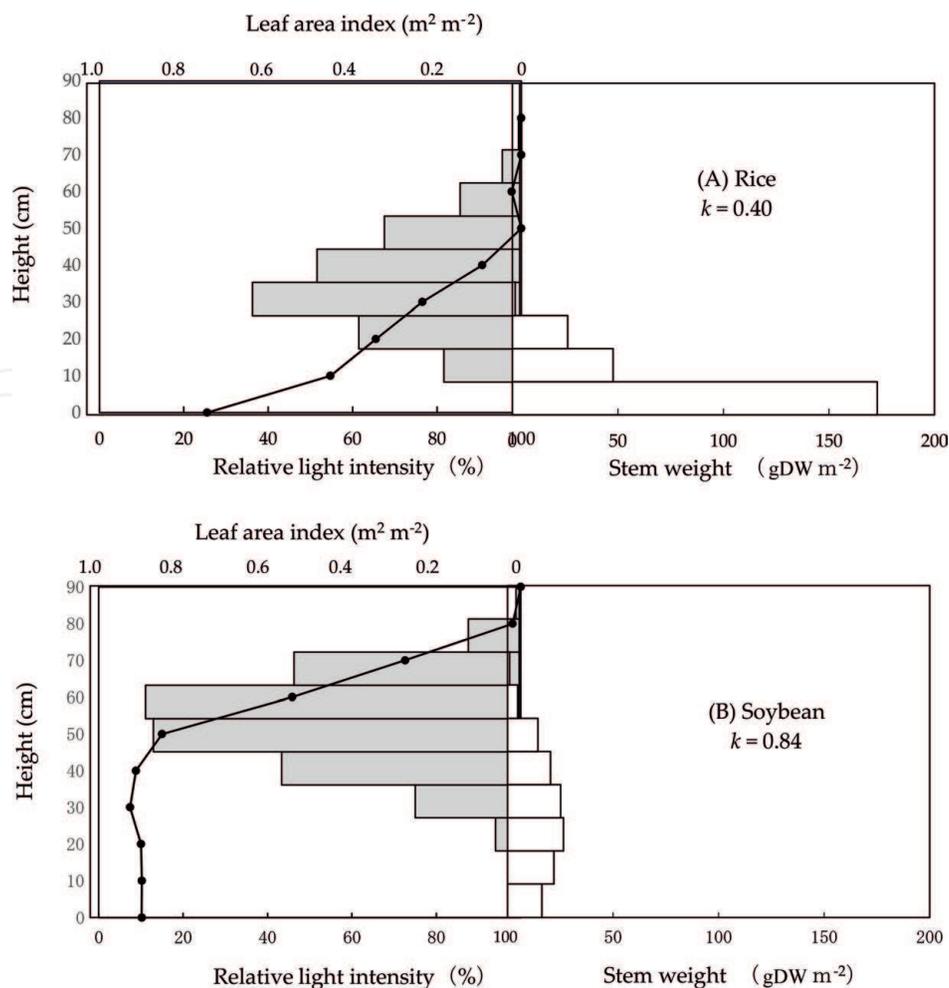


Figure 5.

Vertical distributions of leaf area index and stem dry matter weight (stem weight) of rice (A) and soybean (B) cultivated at Mie Prefecture in Japan just before flowering (original data). Soybean (Fukuyutaka) cultivation and the measurement of dry matter weight, leaf area and relative light intensity were mentioned in the previous study [21]. Young rice seedlings (Koshihikari) were transplanted to the paddy field at a hill spacing of 18 cm and a row spacing of 30 cm ($18.5 \text{ hills m}^{-2}$) on 18 April 2016. Chemical fertilizers (N, P_2O_5 and K_2O) were applied at the rate of 4 g m^{-2} as basal and 1 g m^{-2} as top dressing on June 28. Measurements of the above parameters were made according to that of soybean [21]. The close circle represents relative light intensity inside the canopy. The stem includes leaf sheath (rice) or petiole (soybean). k represents light extinction coefficient.

The light intercepting efficiency (i.e. k) is strongly associated with morphological leaf traits and leaf distribution in the canopy [31]. Among them, leaf erectness is the most distinct determinant of light intercepting efficiency [31]; the improvement of leaf inclination angle by breeding often causes high seed yield in modern rice cultivars. In soybean, however, there is a report that light intercepting efficiency had no influence on canopy photosynthesis [56]. In comparison with Fukuyutaka, Misato-zairai has unstable seed yield, and un-erect and more dense leaves in the uppermost layer of the canopy were found in this cultivar [21]. However, there is no significant difference in light extinction coefficient between these two cultivars [21]. Although light intercepting efficiency may be useful for soybean seed production, the relationship among light intercepting efficiency, its related parameters and seed yield was complicated and unclear [21, 42].

3.3 Leaf orientation adjustment

High light intensity, such as full sunlight, is harmful to plant leaves because high light intensity induces photoinhibition in crop leaves [57]. In leguminous crop plants, including soybean, leaf orientation in the top layer of the canopy changes

during the daytime (paraheliotropism, light avoidant movement [58]), which avoids receiving too much light and, as a result, photoinhibition. This mechanism appears to be turgor-mediated; paraheliotropism is controlled by turgor changes of the pulvinus tissue at the base of leaves [59]. Therefore, paraheliotropism is associated strongly with plant water stress; the degree of the midday avoidance becomes more pronounced in water-stressed plants as compared with well-watered ones [58, 60]. Paraheliotropic response to soil water availability is different between soybean cultivars. Midday leaf angle of the species which grow in the wet habitat is more vertical than that of the species which grow in the dry habitat among wild soybeans from habitats with different water availability [58]. On the other hand, comparison of midday paraheliotropism between two Japanese soybean cultivars exhibited that a major cultivar (Fukuyutaka) with stable seed yield had more vertical midday leaf angle than that of a local cultivar (Misato-zairai) with unstable seed yield and not erect leaves (**Figure 6** [61]).

Leaf angle is composed of the inclination angle of the petiole and the angle between the rachis and leaflets. The latter changes more largely than the former during the daytime (**Figure 6**, [61]), which is associated with paraheliotropism deeply. Meanwhile, there is also cultivar difference in the leaf orientation angle without paraheliotropic leaf movement; for example, this angle of Fukuyutaka is often higher than that of Misato-zairai. However, the correlation between the inclination angle and water content in petiole, which controls leaf orientation angle without paraheliotropism through the turgor change in the pulvinus, is similar in these two cultivars (**Figure 7**) [60]. So, the leaf orientation angle without

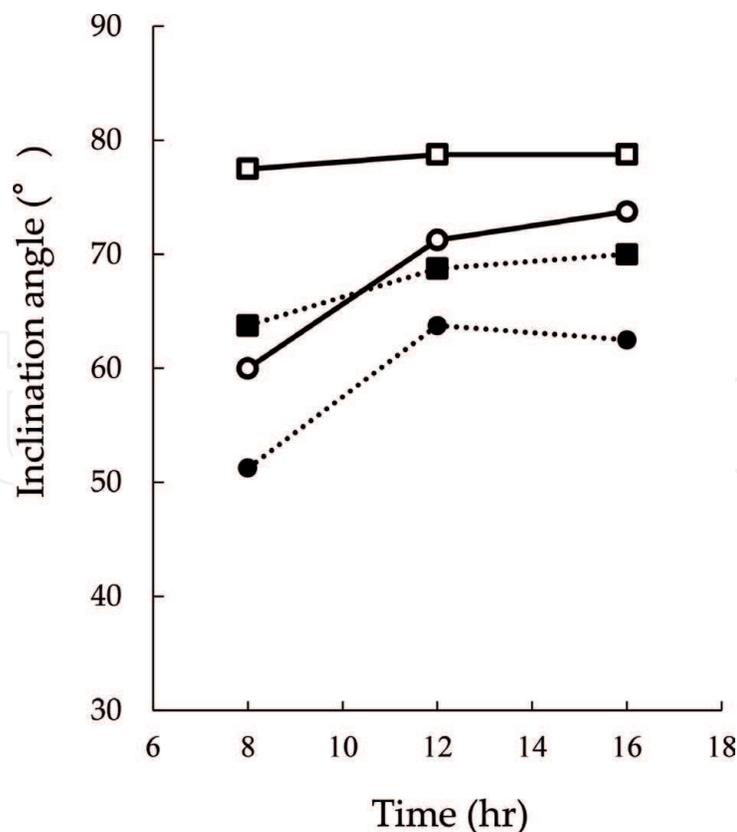


Figure 6. Daily changes in inclination angles of leaflet and petiole in Fukuyutaka (open) and Misato-zairai (close) at beginning bloom (R1). Circle and square symbols represent leaflet and petiole, respectively. The inclination angles of the leaflet and petiole are meant to be the angle between the horizontal plane and the lines from the primary (stem-petiole) pulvinus to the tip of the central leaflet (leaflet) or to the secondary pulvinus (petiole) [61].

paraheliotropic leaf movement would depend on plant water condition through soil water condition and water transport capacity of soybean plants.

3.4 Leaf photosynthesis

Leaf photosynthetic rate means the apparent rate of photosynthetic CO₂ uptake per unit leaf area and is often expressed 'photosynthetic rate' or 'CO₂ exchange rate (CER)'. It is obvious that leaf photosynthesis is an important factor for determining the grain yield through canopy photosynthesis, and high yielding varieties of rice plants often have high leaf photosynthesis and its proper response to top dressing [62].

In Northeast China, it is indicated that leaf photosynthesis is one of the most important genetic contributors to the yield gain through the more plant biomass accumulation during the past 56 years [63]. Similar trends were found in North America [64–66]. For example, the experiment with new and old Canadian cultivars indicated that a 0.52% per yr. increases in leaf photosynthesis and this is a level very similar to the annual yield increase shown by these cultivars [67]. However, there are also conflicting reports on the relationship between leaf photosynthesis and yield; some researchers report only low to moderate correlations [8, 67], and others found no correlation [11, 68, 69]. The association between photosynthesis and yield is likely to be strong during seed filling period (R5–R7). Soybean leaf photosynthesis begins to decline around this period [70, 71], and this decline includes two types: slow and rapid [39]. The conflicting reports on the relationship between leaf photosynthesis and yield may be due to the phenological stage at which the measurements were taken [5]. Leaf photosynthesis is composed of mesophyll photosynthetic capacity and stomatal opening; the latter factor controls leaf photosynthesis through the CO₂ influx into the leaves. Stomatal opening also has another role in controlling H₂O efflux from the leaves; this varies in response to various environmental conditions to avoid excess transpiration and, as a result, leaf water shortage. Therefore, leaf photosynthesis is sensitive to leaf water potential (indicator of leaf water status); leaf photosynthesis of crop plants usually begins to drop in response to the decline in leaf water potential through the decline in stomatal

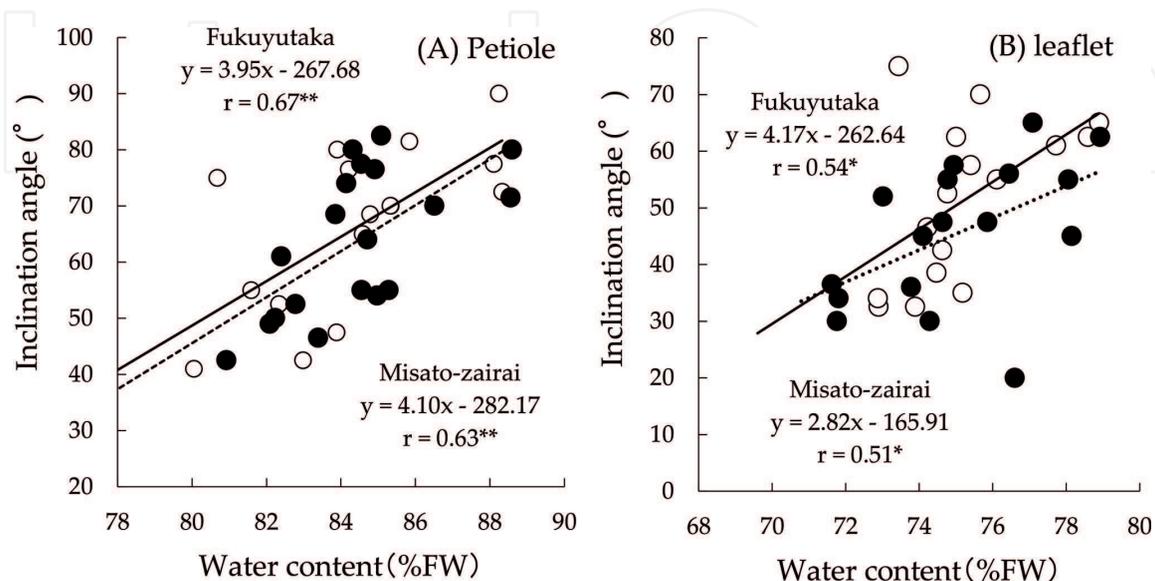


Figure 7. Variation in inclination angles as a function of water content of petiole (A) and leaflet (B) in Fukuyutaka (open) and Misato-zairai (close) at beginning bloom (R1) [60]. r is correlation coefficient. *, **: significant at 5% and 1%, respectively.

conductance (indicator of stomatal opening) [72]. However, the sensitivity of soybean leaves to soil drought is lower; stomatal conductance (indicator of leaf water status) [73] and, as a result, leaf photosynthesis [74] are relatively unaffected until leaf water potential drops below -1.1 MPa and then drops dramatically [73]. These affect strongly the recovery from severe soil drought stress: leaf photosynthesis generally decreases with the decline in stomatal conductance even under mild soil drought condition to avoid excessive water loss from the leaves and severe damage to mesophyll photosynthetic capacity [72]. So, improvement of soil water condition (i.e. precipitation) can cause the recovery of leaf photosynthesis quickly thanks to the maintenance of mesophyll photosynthetic capacity. However, soybean leaves keep high stomatal conductance under relatively severe soil drought condition [73], and this is easy to result in severe damage to mesophyll photosynthetic capacity. In addition, soybean leaves can also keep leaf greenness under severe soil drought condition [52]. So, the symptom of drought stress in soybean leaves is not clear, and the recovery of leaf photosynthesis is impossible if soybean leaves are drooped by severe soil drought. Similarly, soybean leaf senescence can occur without a concomitant loss of leaf greenness [5]. It is too difficult to measure the net leaf photosynthetic capacity and to evaluate the relationship between leaf photosynthesis and yield accurately.

4. Yield and yield components

The increase in the potential capacity of photoassimilate supply (source) is an important matter for high crop yield; however, high yield results not only from the increase in source alone but also from the potential capacity of photoassimilate acceptor (sink). The sink accepts and consumes the photoassimilate for its own growth and maintenance. Soybean major sink is the economically important harvest components (seed); soybean seed yield can be expressed as the function of yield components as follows:

$$\text{Yield} = \text{Pod number} \times \text{Seed number per pod} \times \text{Seed size}$$

Seed size (g per seed) is also expressed as 100 seed weight. Pod number (no. m^{-2}) can be separated into plant density (hill number, plant m^{-2}) and pod number per plant (no. plant^{-1}); plant density is relatively easy to control among yield components through sowing. Meanwhile, pod number can be also separated into pod per reproductive node (no.), reproductive node number per area (no. m^{-2}), percent reproductive nodes (%) and node number per area (no. m^{-2}). Many researchers examine the determinant period of seed yield in relation to the manipulation of light interception by shading, defoliation and wide row spacing at various growth periods and indicate that light interception during the period between R1 and R6 affects seed yield strongly through the response of pod and seed number [75]. Sink capacity is like a process of photoassimilate accumulation in a container; high volume for accumulation can accept a large amount of photoassimilate, and this results in high seed yield. Similar to other crop plants, seed number plays a determinant role in sink capacity, and this increase is often associated with high seed yield (**Figure 2B**) [75]. The period between R1 and R6 determines two numbers; pod number is determined critically by light interception during the period between V5 and R3 [39] and seed number is during R3–R6 [76]. Although pod number does not control seed yield as strongly as seed number (**Figure 2A, B**), the occurrence of seed number depends on pod number and reproductive closely (**Figure 2C**). High

canopy photosynthesis during the period between R1 and R6 would affect soybean seed yield with the increase in pod number and seed number.

Sink capacity is also associated with source in a volumetric flow of photoassimilate, phloem loading and unloading. For example, the removal of wheat ear at grain filling period reduced about 50% flag leaf photosynthesis within 3–15 h, and the outflow of ^{14}C -labeled assimilates from the flag leaves (indicator of loading) also reduced remarkably [77]. Sink activity such as formation of flower, pod and seed is sensitive to environmental stress, and this decline decreases leaf photosynthesis through the restriction of phloem loading. Maintenance of sink activity contributes to high yield not only by the increases in pod number and seed number but also by activating leaf photosynthesis. However, another major sink, *Rhizobium japonicum* in the root nodules of soybean plants, is more sensitive to environmental condition than the host plants. For example, respiration of root nodules decreases below -0.4 MPa of root nodule water potential [78] even though leaf photosynthesis is kept until -1.1 MPa of leaf water potential. Root nodules consume much photoassimilates to fix atmospheric nitrogen into ammonium and subsequently ureides for long-range transport [79]. The major source of nitrogen accumulation is atmospheric nitrogen fixation by root nodule [80]; 100% (Brazil) [81] or 40–50% (Midwestern United States) [82] of nitrogen need depends on biological nitrogen fixation. The decline in root nodule activity would decrease not only canopy photosynthesis and seed filling directly by nitrogen deficiency but also leaf photosynthesis indirectly through the restriction of phloem loading and unloading, and this may be associated with the complex of soybean seed production.

5. Conclusion

As mentioned above, the researches about the relationship between seed production, yield components and canopy photosynthesis have been conflicted, and there is no worldwide universal theory for high yield. Even in Japan the strategy for high yielding is different; high biomass is useful for high yield in north Japan, and early sowing is tried to get high biomass [83]. However, high biomass often causes lodging and results in low yield in west Japan [84]; partial defoliation of above ground before blooming is recommended to avoid high biomass in Aichi Prefecture [84]. In the other major crops such as rice, maize and wheat, semidwarf gene plays an important role in high yield, and this introduction by breeding contributes to a dramatical increase of world grain yield [31, 85]. Dwarfing is also useful for soybean seed production; however, this factor alone cannot contribute to high yield. Soybean plants itself have acclimated flexibly to various environmental conditions, and the soybean cultivation countries increased about two times from 1961 to 2016 [86]. Realization of worldwide cultivation may be associated with the construction of independent growth and seed production proper to the area and its climate; therefore, it would be necessary for high soybean yield not only to expect the worldwide universal theory for high yield but also to build the own theory for each area in consideration of growth features and climate.

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