# SOYPOD: A Model of Fruit Set in Soybean

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## ABSTRACT

**The soybean [*Glycine max* (L.) Merr.] plant matches its reproductive potential to environmental conditions by adjusting the number of fruits and seeds that it produces. This adjustment is an important, but not well understood, part of the yield production process. Developing a model of fruit set will contribute greatly to a better understanding of the determination of fruit number and yield. The model (SOYPOD) is based on the well documented principle that fruit number is related to assimilate availability during flowering. Inputs, including daily photosynthesis, flower production, and potential pod and seed growth rates, were taken from field and greenhouse experiments. Fruit survival at an isolated node was determined by comparing the daily assimilate supply with the assimilate requirement of the developing fruits, which are sensitive to supply only until the pod wall reaches its maximum size. Abortion occurs when the fruit does not receive assimilate for ABRTM consecutive days during the sensitive period (SEN). The most mature fruits receive assimilate first when assimilate is limiting. It was possible to find realistic combinations of ABRTM and SEN that mimicked the curvilinear response of fruit number to increasing assimilate supply observed in planta. Increasing the individual seed growth rate decreased fruit number when the assimilate supply was held constant, as it does in planta. SOYPOD accurately mimics the fruit set process at isolated nodes in soybean suggesting that it can be used as the basic building block of a whole plant model.**


The yield of grain crops is determined by the dry matter accumulated by the seeds during seed filling. All plant processes that affect yield (e.g., photosynthesis, respiration, partitioning, etc.) must ultimately express their effect through the seeds. Variation in the number of seeds per unit area is responsible for much of the environmentally induced variation in soybean yield (Egli, 1998; Calvino et al., 2003) and the yields of other grain crops, such as maize (*Zea mays* L.) (Jong et al., 1982), sunflower (*Helianthus annus* L.) (Cantagallo et al., 1997), wheat (*Triticum aestivum* L.) (Frederick et al., 2001; Peltonen-Sainio et al., 2007), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), and rye (*Secale cereale* L.) (Peltonen-Sainio et al., 2007). This pre-eminent ranking occurs because the determination of seed number represents the first opportunity for the crop to adjust its reproductive output to environmental conditions.

Fruit and seed number in most crops are intimately linked to photosynthesis during the early stages of reproductive growth and to the characteristics of the developing seed (Egli, 1998, 2006). Modification of photosynthesis by manipulating, for example, solar radiation, leaf area, $CO_2$ concentration, or water and N availability during flowering and fruit set in soybean usually results in corresponding changes in the number of fruits and seeds at maturity (Shaw and Laing, 1966; Hardman and Brun, 1971; Brevedan et al., 1978; Schou et al., 1978; Egli and Zhen-wen, 1991; Board and Tan, 1995; Jiang and Egli, 1995). Soybean genotypes that produce small seeds with low seed-growth rates produce more fruits and seeds at a given level of assimilate availability than genotypes that produce large seeds with high seed-growth rates (Egli and Zhen-wen, 1991; Egli, 1993; Bruening and Egli, 1999). This inverse relationship between seed-growth rate and fruit and seed number was also apparent in comparisons among mung bean (*Vigna radiate*), peanut (*Archis hypogaea* L.), and cowpea (*Vigna unguiculata* L.) (Charles-Edwards et al., 1986).

## Flowering and Fruit Set

The flowering and fruit set process at the community level in soybean is extraordinarily complex across time and space. Assuming a typical yield level, seed size, and 50% flower and fruit abortion, the process involves the production of 700 fruits $m^{-2}$ from 1400 flowers $m^{-2}$ borne on roughly 500 nodes during a 30- to 50-d period. Development of a girdled-node technique (Bruening, 1997; Bruening and Egli, 1999, 2000; Egli and Bruening, 2002a, 2002b) decreased the complexity by making it possible to study flower production and fruit set at a single isolated node without interference from activity at other nodes.

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**Abbreviations:** ABRTM, number of consecutive days without assimilate required to trigger fruit abortion; ASMAX, maximum amount of unused assimilate that can be returned to the assimilate pool each day (mg glucose equivalents); LAGP, the length of the lag phase of pod dry weight accumulation (days after flower opening); LAGS, the length of the lag phase of seed dry weight accumulation (days after flower opening); PDW, pod wall dry weight (mg $fruit^{-1}$); SDW, seed dry weight (mg $seed^{-1}$); SEN, length (days after flower opening) of the period when fruit survival is sensitive to assimilate supply; SGR, seed growth rate.

Flowers at a single girdled node are produced for 30 to 35 d, with the first group produced on the main raceme and a second group on sub-branches (Egli and Bruening, 2002a). Late-developing flowers at a node are much more likely to abort than those developing earlier (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986a; Egli and Bruening, 2002a), and removal of early flowers or fruits decreases abortion of late-developing flowers and fruits (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986a). Increasing the synchrony of flowering at phloem-isolated nodes increases fruit set (Egli and Bruening, 2002b). Flowers and small fruits are the most likely candidates for abortion; fruits that reach their maximum length rarely abort (Heitholt et al., 1986a; Egli and Bruening, 2006), and small seeds are more likely to abort than those in the linear phase of growth (Duthion and Pigeaire, 1991; Westgate and Peterson, 1993).

The response of fruit and seed number at isolated nodes to increasing photosynthesis was decidedly curvilinear (Bruening and Egli, 1999, 2000), in contrast to the linear response of plant communities (Egli and Zhen-wen, 1991; Egli, 1993; Ball et al., 2000). The number of fruits at girdled nodes approached saturation at roughly 20 to 40% of maximum photosynthesis, and the curvilinear response was not a result of a lack of flowers because up to 80% of the flowers failed to develop into mature pods at maximum photosynthesis rates (Bruening and Egli, 1999, 2000). Bruening and Egli (1999) and Egli and Bruening (2002a, 2002b) suggested that competition for assimilate among fruits of different ages produced the curvilinear response. Assimilate utilization by the early fruits and seeds that are growing rapidly may reduce assimilate availability to the small, late-developing fruits to a level that precludes additional fruit set (Bruening and Egli, 1999). Reducing competition between early and late fruits by increasing the synchronony of flowering increased fruit number (Egli and Bruening, 2002b), suggesting that the timing of flower development is an important determinant, in addition to assimilate supply and sink characteristics, of fruit number in soybean (Egli and Bruening, 2002a).

A thorough understanding of the mechanisms responsible for the adjustment of fruit and seed number to the productivity of the environment is needed to produce a complete description of the yield production process. More than 75 yr of research have documented and described many aspects of flowering and fruit set in soybean, but its complexity has made it difficult to develop a detailed mechanistic understanding of the process. Constructing a model of the fruit set process would be one way to deal with this complexity.

The objective of this study was to develop a mechanistic simulation model of fruit set at an isolated node of soybean to investigate the relative importance of the individual processes hypothesized to determine if a flower survives to produce a mature fruit. This model (SOYPOD) is primarily based on concepts and principles developed in a series of investigations of fruit set at girdled nodes (Bruening, 1997; Bruening and Egli, 1999, 2000; Egli and Bruening, 2002a, 2002b) and on intact plants (Egli and Bruening, 2006). The model is not intended to predict fruit and seed number as a function of environmental conditions but rather, as described by McCree and Fernandez (1989), to serve as an experimental tool to investigate the overall process. If the model can accurately mimic the fruit set process, systematic manipulation of the model will provide a better understanding of the importance of each component and their interactions, especially those processes that cannot be manipulated experimentally. A successful model at the isolated–node level can also be used to assemble a model of fruit set at the whole plant–plant community level.

## MATERIALS AND METHODS

### Model Description

The model (SOYPOD) simulates fruit set at a single isolated soybean node—isolated in the sense that the leaf at that node is the only source of assimilate (i.e., there is no import from or export of assimilate to other nodes) (Bruening and Egli, 1999). Modeling an isolated node avoids the complexities introduced by activity at other nodes, making it much easier to construct a model at the individual fruit level.

The model is based on the well accepted concept that fruit survival is a function of assimilate availability, which was used by earlier modelers of fruit and seed set (Sheldrake, 1979; Charles-Edwards, 1984; Charles-Edwards and Beech, 1984; W.G. Duncan [cited in Egli, 1998]) and in many crop simulation models (Boote et al., 1998; Ritchie and Wei, 2000; Lizaso et al., 2001; Weiss and Moreno-Sotomayor, 2004). The model operates on a daily time step and each day the assimilate requirement of the developing fruits is compared with the assimilate available from photosynthesis and fruits that do not receive assimilate begin the abortion process (Fig. 1). Many crop simulation models relate some measure of assimilate availability during flowering and seed set to total seed number at maturity. Others, principally CROPGRO (Boote et al., 1998), include a more detailed consideration of fruit growth that is somewhat similar to the approach used here.

Photosynthesis (mMol $CO_2$ $node^{-1}$ $d^{-1}$) for each day is supplied by an input file containing estimates of photosynthesis from greenhouse experiments with isolated nodes (cultivar Elgin 87) (Egli and Bruening, 2002b). The assimilate supply in planta may also include contributions from stored carbohydrates, principally starch, in leaves and other plant parts, that are mobilized in response to fluctuations in supply and demand (Huber et al., 1984; Bruening and Egli, 2000). Involvement of stored carbohydrates is simulated in SOYPOD by returning unused assimilate to the assimilate pool for use the next day. The supply of assimilate, therefore, on any given day is assimilate available from photosynthesis and that was not used previously. The maximum amount of unused assimilate that can be returned to the assimilate pool on each day is set by ASMAX (mg glucose equivalents). The relationships in Boote et al. (1998) were used to convert the photosynthesis data into glucose equivalents for comparison with fruit growth.

Flower production on each day is supplied by an input file that contains daily flower production data from the greenhouse experiments supplying photosynthesis data (Egli and Bruening, 2002a) (Fig. 2). The identity of each flower and its fruit and its age (days after flowering) is maintained in the fruit file during the execution of the model, producing a suite of fruits of different ages competing for assimilate on each day.

## Fruit Growth

The assimilate requirement of each fruit is determined by the rate of dry matter accumulation of pod walls and seeds (Fig. 3), which was estimated from data collected by sampling marked pods over time (cultivar Elgin 87) in a field experiment (D.B. Egli, unpublished data, 1996).

Pod wall dry weight (PDW) as a function of time (days after the flower opened [d]) is determined by Eq. [1] during the lag phase and by Eq. [2] when the lag phase ends. The length of the lag phase (LAGP) is set equal to SEN – 20 so the maximum pod weight always occurs early in seed growth as SEN is changed. Equation [1] is used if d ≤ LAGP, otherwise Eq. [2] is used to calculate pod wall dry weight.

$$\text{PDW (mg fruit}^{-1}) = (4.345/\text{LAGP})\text{d} \quad [1]$$

$$\text{PDW} = 143.7114/[1 + \exp - (\text{d} - 11.2855)/3.255] \quad [2]$$

Seed dry weight (SDW) follows Eq. [3] during the lag phase of growth and Eq. [4] during the transition between the lag and linear phases of growth, and it increases at a constant rate (usually set at 6.20 mg seed$^{-1}$ d$^{-1}$) during the linear phase of growth. The length of the lag phase of seed growth (LAGS) is adjusted to match pod growth when SEN is changed by setting LAGS = SEN – 9. Equation [3] is used when d ≤ LAGS. The transition (Eq. [4]) is used for d > LAGS to d = (LAGS + 6). The linear phase begins with LAGS + 7.

$$\text{SDW (mg seed}^{-1}) = (0.1032/\text{LAGS})\text{d} \quad [3]$$

$$\text{SDW} = 0.2278 - (0.4161\ \text{d}) + (0.2920\ \text{d}^2) \quad [4]$$

These equations set maximum fruit growth rates; actual growth rates depend on the availability of assimilate. All fruits were assumed to contain three seeds, so total fruit weight at any time is the summation of PDW and (SDW × 3). Seed growth is terminated when the dry weight of an individual seed is 160 mg seed$^{-1}$ or greater. The growth rate on day d was the difference between the fruit dry weight on day d and d–1.

Pod and seed growth rates are converted to glucose equivalents to facilitate comparisons with the assimilate supply from photosynthesis using the relationships in Boote et al. (1998). Seeds were assumed to contain 398 mg g$^{-1}$ protein, 197 mg g$^{-1}$ oil, and 357 mg g$^{-1}$ carbohydrates, whereas the composition of the pod walls was set at 250 mg g$^{-1}$ protein, 15 mg g$^{-1}$ oil, and 656 mg g$^{-1}$ carbohydrate (Wilkerson et al., 1983).

## Fruit Survival

Fruit survival in SOYPOD is determined by comparing the assimilate supply (photosynthesis from the input file plus retained assimilate from the previous day) and the needs of the developing fruit computed from the curves in Fig. 3. This comparison is governed by the following three rules (Fig. 1):

1. Developing fruits are sensitive to the assimilate supply until the pod wall reaches its maximum length and weight, which usually occurs near the beginning of the linear phase of seed growth (Egli et al., 1981; Heitholt et al., 1986a; Egli, 1998; Egli and Bruening, 2006). At the end of the sensitive period, the fruit no longer aborts. The length of the sensitive period, which begins when the flower opens, is given by SEN (days). When SEN varied, it was necessary to adjust the length of the lag phase

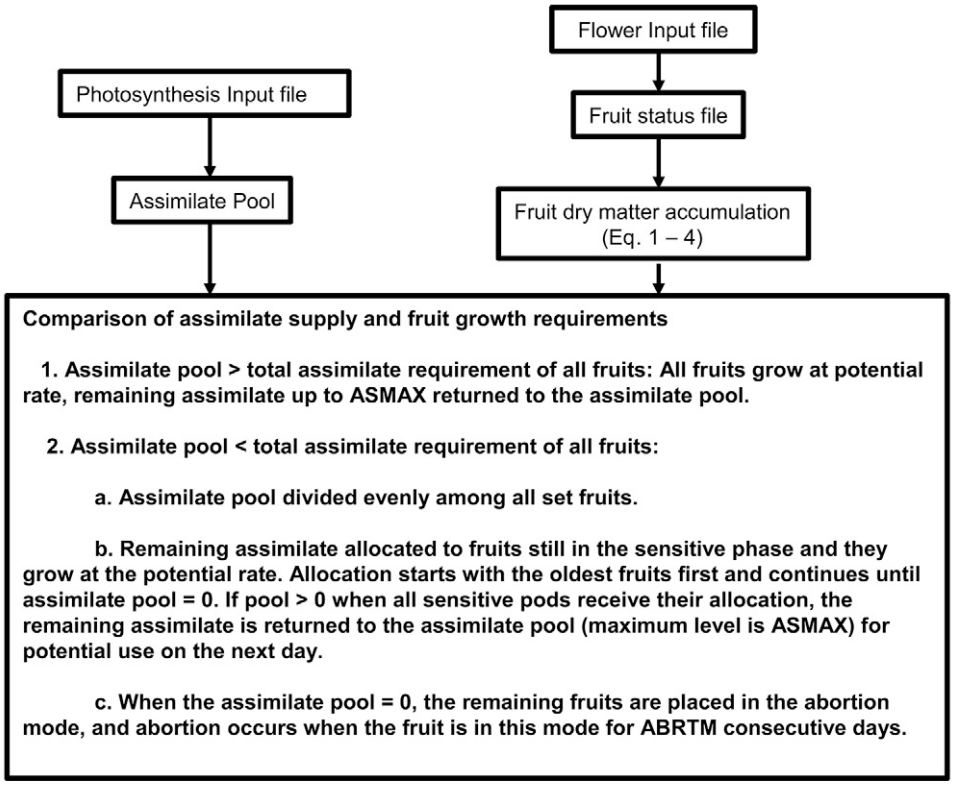


**Fig. 1. Simplified flow chart of SOYPOD. The model operates on a daily time step, and daily photosynthesis and flower production data come from input files. The age and current status (in the sensitive phase, set, in the abortion process, aborted) of each fruit is cataloged in the fruit status file.**

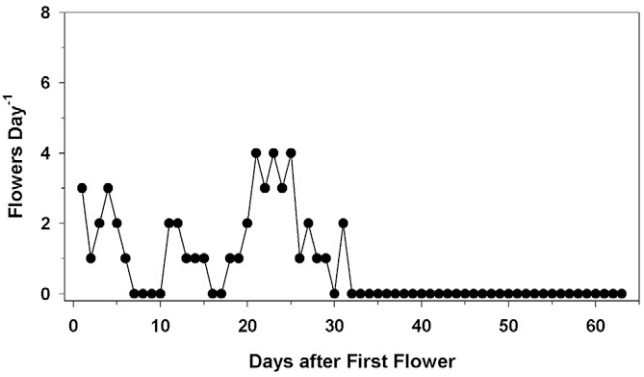


**Fig. 2. Flower production profile used as input to SOYPOD. Data from the one girdled-node treatment in Experiment 2 are from Egli and Bruening (2002a).**

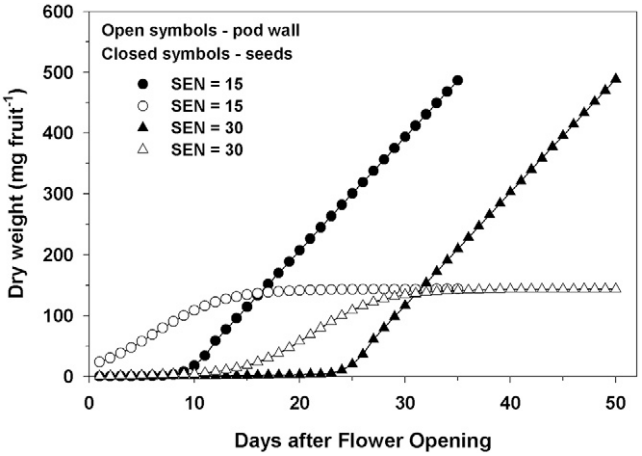


**Fig. 3. Dry matter of the pod wall and seeds as a function of days after flowering. These curves, based on data from marked pods of 'Elgin 87' growing in the field, are used to estimate growth rates and assimilate requirements of developing fruits in SOYPOD. SEN defines the period during the initial phase of pod growth when the pod is sensitive to assimilate supply. The period extends from flower opening until the pod wall reaches its maximum length and weight early in seed filling.**

of pod wall and seed growth to maintain the occurrence of maximum pod wall weight near the end of SEN (Fig. 3). If the fruit survives to the end of the sensitive period, it is considered "set" and will survive until maturity, although its growth rate depends on assimilate availability up to the potential rate set by Eq. [1–4].

2. A fruit that receives no assimilate for a specified number of consecutive days (ABRTM) during its sensitive phase aborts and is irretrievably lost. These fruits are not included in further calculations by the model. The count begins on the first day the fruit receives no assimilate and continues until it equals ABRTM (triggering abortion) or the fruit receives assimilate again (count is set to zero). Several researchers have shown that abortion requires more than 1 d of assimilate deprivation (Weibold, 1990; Egli and Bruening, 2006), but the length of ABRTM is not well defined.

3. Each day's assimilate supply is partitioned among developing fruits as follows:

   a. If the assimilate supply is greater than or equal to the combined growth rate of all fruits, they all grow at the potential rate determined by the curves in Fig. 3 and the age of the fruit. Leftover assimilate may be retained in the assimilate pool up to the level set by ASMAX.

   b. If the assimilate supply is less than the combined growth rate of all fruits, the assimilate is divided among the fruits as follows: first, it is divided among the "set" fruits (fruits that reached the end of the sensitive period without aborting), and they all grow at the potential rate or at proportionately lower rates if the supply is less than the total potential rate of the set fruits. Assimilate not used by "set" fruits is allocated to fruits still in the sensitive phase, and each fruit, starting with the oldest, receives enough assimilate to grow at the potential rate until the assimilate supply is exhausted. The remaining fruits get no assimilate and are placed in the abortion mode where, after ABRTM consecutive days without assimilate, they abort.

These priorities are based on evidence that reproductive failure commonly involves flowers or immature fruits (Heitholt et al., 1986a; Egli and Bruening, 2006), suggesting that younger fruits have a lower priority for assimilate, causing them to abort more frequently.

The fate of each fruit is noted, and the daily time step continues until the fate of the last fruit is determined SEN days after the last flower opened.

No attempt was made to model the many other aspects of plant growth that potentially influence the assimilate available for fruit set, such as respiration, N metabolism, partitioning, and growth of non-fruit structures. Temperature influences fruit growth rates (Egli and Wardlaw, 1980), whereas temperature and photoperiod influence flower production and survival (van Schaik and Probst, 1958; Zheng et al., 2002). Many of these processes are involved in determining the supply of assimilate to individual fruits and/or the rate of fruit growth and hence fruit set. There is not enough information available to rationally model their effects at the level addressed by SOYPOD. Equating the assimilate supply to photosynthesis (plus stored assimilate) without adjusting for other uses influences the absolute fruit number predicted by the model, but it probably has little affect on the dynamics of fruit development and survival, which is the primary focus of SOYPOD.

## RESULTS AND DISCUSSION

### Model Evaluation

Accurate estimates of the critical parameters SEN and ABRTM are not available in the literature. Consequently, various combinations of these parameters were evaluated in SOYPOD (Fig. 4 and 5) to identify those that mimicked the observed response of fruits at isolated nodes to changes in photosynthesis (Bruening and Egli, 1999, 2000). Variation in photosynthesis was created by multiplying daily photosynthesis from the input file by a fraction ≤1.0 to create relative photosynthesis.

The number of fruits responded to increasing photosynthesis for all combinations of SEN, ABRTM, and ASMAX, but the pattern of the response depended on the levels of the three parameters (Fig. 4 and 5). Saturation curves were more common and maximum fruit number increased as ABRTM

increased when SEN ≥ 20 d. Some of these curves at both levels of ASMAX matched the shape of curves reported by Bruening and Egli (1999, 2000), including a second increase at maximum photosynthesis rates. Many of these curves reached saturation at 20 to 50% of maximum photosynthesis, which agrees with the field and greenhouse experiments of Bruening and Egli (1999, 2000) in which the supply of assimilate was varied by defoliation.

Allowing stored assimilate to participate in fruit set (i.e., setting ASMAX at 300 mg glucose equivalents, which is roughly 1.5 times the average daily input from photosynthesis) had some effect on the shape of the response curve but had little effect on maximum fruit number (Fig. 4 and 5), with the largest advantage occurring when SEN = 30 d and ABRTM = 24 d (an increase of only 11%).

The levels of SEN (20–30 d) and ABRTM (12–24 d) that mimicked the observed responses to increasing photosynthesis most closely were in the range of the few estimates in the literature. The sensitive period when the fruit is susceptible to assimilate deprivation (SEN) ends when the pod reaches its maximum length (Egli, 1998; Egli and Bruening, 2006). This occurs approximately 12 to 30 d after the flower opens (Yoshida et al., 1983; Zheng et al., 2002; Egli and Bruening, unpublished data). Direct estimates of ABRTM are not available, but Egli and Bruening (2006) found that little abortion occurred after 4 d of shade-induced assimilate deprivation (80% shade) and that 12 to 16 d were required for abortion levels to equal those on a continuous shade treatment. Weibold (1990) found that abortion of late flowers on a raceme could be reduced by removal of basal flowers up to 11 d after the late flower opened. These results suggest that a developing fruit can withstand up to 2 wk of assimilate deprivation before the abortion processes is complete.

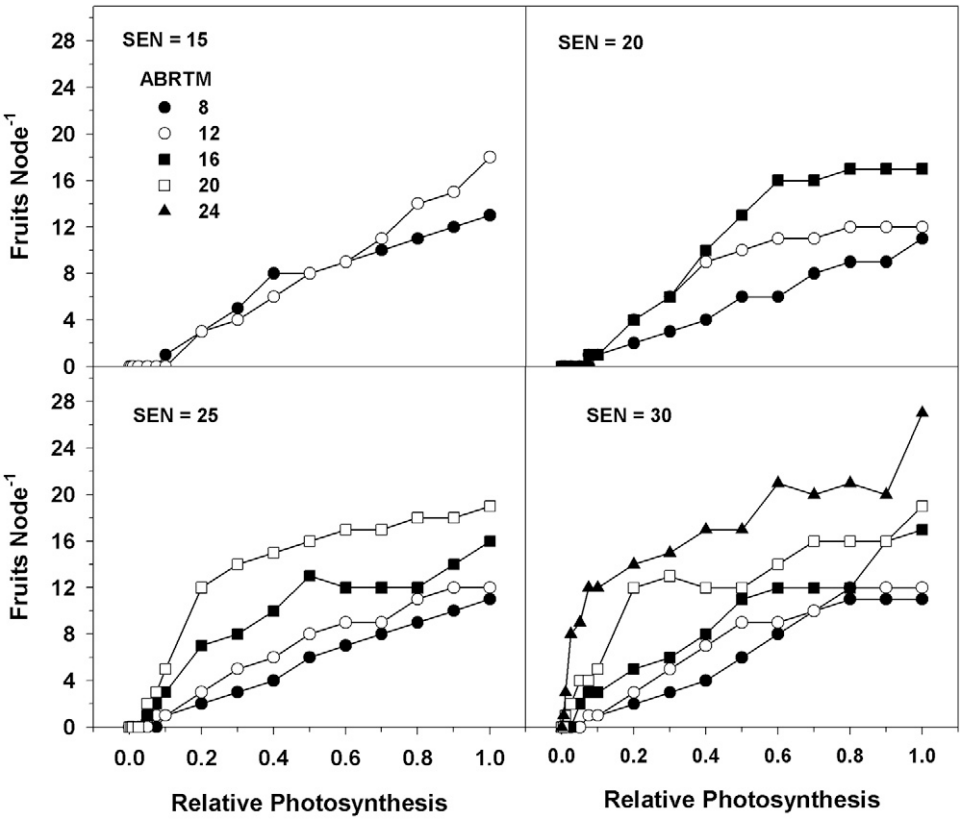


**Fig. 4. Simulated relationship between photosynthesis and fruits per node from SOYPOD with ASMAX = 0 mg glucose equivalents and seed growth rate = 6.20 mg seed$^{-1}$ d$^{-1}$. Photosynthesis and flower profile input data from the one girdled-node treatment in Experiment 2 are from Egli and Bruening (2002a).**

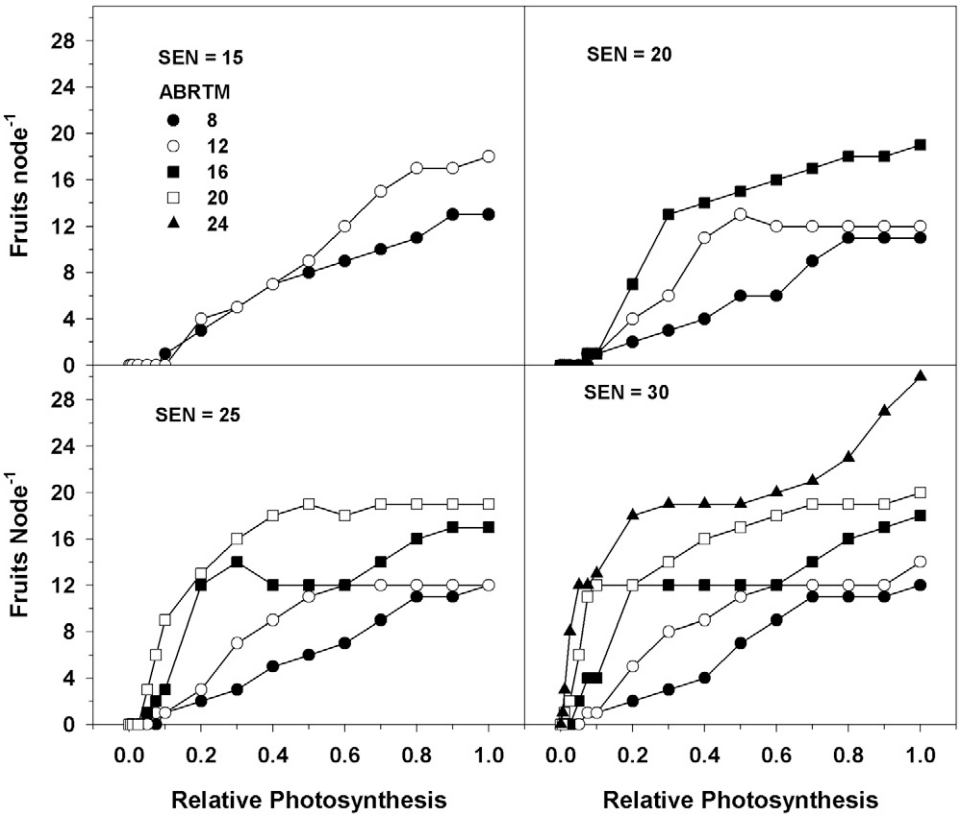


**Fig. 5. Simulated relationship between photosynthesis and fruits per node from SOYPOD with ASMAX = 300 mg glucose equivalents and seed growth rate = 6.20 mg seed$^{-1}$ d$^{-1}$. Photosynthesis and flower profile input data from the one girdled-node treatment in Experiment 2 are from Egli and Bruening (2002a).**

**Table 1. Measured and predicted fruit set at isolated nodes from two greenhouse experiments, Cultivar Elgin 87. Observed data are from Egli and Bruening (2002a, 2002b).**

| Exp. | Mean photosynthesis† | Flowers | Observed fruits | Predicted fruits‡ 25/16§ 0¶ | 25/16§ 300 | 30/20 0 | 30/20 300 |
|---|---|---|---|---|---|---|---|
| | Mmol $CO_2$ $node^{-1}$ $d^{-1}$ | no. $node^{-1}$ | | | | | |
| 2 | 13.9 | 48 | 11.9 | 16 | 17 | 19 | 20 |
| 3 | 19.6 | 59 | 19.1 | 17 | 25 | 23 | 35 |

† During flowering and pod set.

‡ Predicted by SOYPOD using flowering profiles and daily photosynthesis from each experiment.

§ SEN/ABRTM.

¶ ASMAX in mg glucose equivalents.

The model not only responded as expected to changes in photosynthesis within experiments; it also responded to variation between experiments (Table 1). Measured photosynthesis during flowering and pod set was 41% higher in Experiment 3 (Egli and Bruening, 2002a, 2002b) than inExperiment 2, resulting in more flowers and 60% more surviving fruits. SOYPOD predicted this increase in fruit survival when it was supplied with flower and photosynthesis data from Experiments 2 and 3, although the response depended on the levels of SEN, ABRTM, and ASMAX (the largest responses [47 and 75%] occurred with SEN/ABRTM set at 25/16 and 30/20 and ASMAX at 300 mg glucose equivalents; Table 1). The availability of stored assimilate (i.e., ASMAX = 300 mg glucose equivalents) increased fruit number in Experiment 3 but not in Experiment 2. Predicted fruit numbers were usually higher than observed; more accurate predictions are probably not possible without a more detailed modeling of the proportion of the total assimilate supply that is available for fruit set.

Fruit number in soybean is also related to genetic variation in individual seed growth rate (SGR, the rate of dry matter accumulation by an individual seed during the linear phase of seed growth). With a constant assimilate supply, increasing SGR causes compensatory decreases in fruit and seed number on intact plants (Egli and Zhen-wen, 1991; Egli, 1993, 2006) and at isolated nodes (Bruening and Egli, 1999). Increasing SGR in SOYPOD from 3.0 to 17.0 mg $seed^{-1}$ $d^{-1}$ (this range includes much of the reported variation in SGR in soybean [Egli, 1981]) while maintaining a constant assimilate supply caused fruit number to decrease (Fig. 6). The response was similar to that found in experiments with three cultivars with genetic differences in seed size and SGR (Bruening, 1997; Bruening and Egli, 1999).

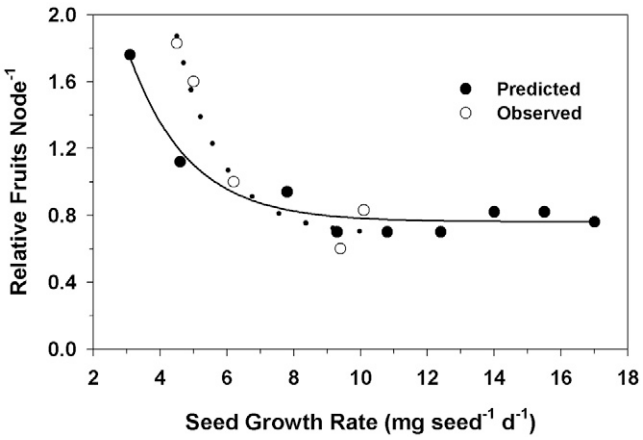


**Fig. 6. The relationship between seed growth rate (SGR) and fruits per node. Observed data from Bruening and Egli (1999) include three cultivars and 2 yr in the field. The predicted data are from SOYPOD (SEN = 25, ABRTM = 16, ASMAX = 0) with photosynthesis and flower data from the one girdled-node treatment in Experiment 2 from Egli and Bruening (2002a). Relative fruits per node were calculated for each experiment by setting the fruits per node for a seed growth rate of 6.20 mg $seed^{-1}$ $d^{-1}$ equal to 1.0 to adjust for differences in photosynthesis between experiments. Both regression analyses were significant at $P = 0.01$.**

SOYPOD successfully mimicked observed effects of variation in photosynthesis (within and between years) and SGR on fruit number. Assimilate availability is the driving force in the model, but the dynamics of fruit development and seed characteristics play important roles in determining fruit number (Fig. 4–6). All of these relationships are solidly based on experimental evidence, and, when they were combined in SOYPOD, they produced a model that accurately mimicked critical aspects of the in planta fruit set process.

A major weakness in the model stems from our inability to accurately quantify and therefore model the assimilate supply that determines fruit survival (Heitholt et al., 1986b). Consequently, the relationship between assimilate supply and fruit number is based on a general association between the two characters. Even in a simple single leaf–node system, it is unlikely that all of the photosynthate will be available to set fruit, but accurately modeling this partitioning is not possible. SOYPOD cannot be expected to accurately predict absolute fruit number in planta without an accurate depiction of the assimilate supply available to the individual fruit.

There was no unique combination of SEN and ABRTM that mimicked measured responses; rather, it seemed that the greatest deviation from curves in the literature (Bruening and Egli, 1999, 2000) occurred with the smallest ABRTM. Maximum fruit number increased as the difference between the two parameters decreased, and SEN/ABRTM = 1.25 always produced maximum fruit number at each level of SEN. The greatest absolute fruit number occurred with SEN = 30 and ABRTM = 24.

Little is known about the magnitude or variation in ABRTM, except that ABRTM is much greater than 1 (Weibold, 1990; Egli and Bruening, 2006). More is known about SEN. There is evidence that it is affected by photoperiod and the timing of flower development and that it varies among species and among cultivars within a species (Saitoh et al., 1998; Zheng

et al., 2002). The magnitude of SEN and ABRTM was important, but the practical significance of these choices cannot be determined without additional knowledge of ABRTM—How much does it vary, what causes it to vary, and does it vary in conjunction with SEN to maintain a constant ratio?

Allowing SOYPOD to "store" assimilate for later use in the fruit set process (i.e., ASMAX > 0 mg glucose equivalents) affected the response of fruit number to increasing photosynthesis (Fig. 4 and 5), but the increase in fruit number was relatively modest (the maximum advantage was 17%, and it was often <10%; Fig. 4 and 5). The response in Table 1 (Experiment 3) was considerably larger. The failure of predicted fruit number to consistently respond to stored assimilate is consistent with the argument, advanced on theoretical grounds, that the numbers of fruits and seeds are primarily a function of current assimilate (Egli, 1998) This is a logical conclusion if one accepts the assumption that total seed growth rate (g $m^{-2}$ $d^{-1}$) should be matched with the capacity of the canopy to fill the seeds (i.e., daily photosynthesis [g $CO_2$ $m^{-2}$ $d^{-1}$]) to prevent sink limitations or the production of smaller-than-normal seeds. It is not clear why the response to stored assimilate was larger in Experiment 3 than in Experiment 2 (Fig. 4 and 5).

The response of SOYPOD to external stimuli (changes in photosynthesis and seed growth rate) mimicked the in planta fruit set process at an isolated node. This concordance does not prove that the plant follows the rules used in SOYPOD, but it does suggest that these rules may provide a reasonable approximation of the processes that determine the fate of individual fruits. The functionality of SOYPOD suggests that it may be a potentially useful tool to investigate flower production and fruit survival and particularly those aspects of the process that cannot be easily manipulated experimentally.

## Evaluation of Variation in Flower Production and Assimilate Supply

### Flower Production

The high levels of flower and pod abortion usually found in soybean (van Schaik and Probst, 1958; Hansen and Shibles, 1978; Jiang and Egli, 1993) seem to suggest that the availability of flowers does not limit fruit number in this crop, although Dybing (1994) suggested that this conclusion may represent an oversimplification. I evaluated the importance of flower number at isolated nodes with SOYPOD by multiplying the daily flower production from the input file by a factor greater than 1.0. This procedure increased flower number while maintaining the original temporal distribution. Flower production at a single node is decidedly biphasic (Munier-Jolian et al., 1994; Egli and Bruening, 2002a), so the increase was applied only to the early flowers (i.e., those on the main raceme produced between Day 1 and 8 [Fig. 2]) or only to the late flowers (i.e., those on the sub-branches produced after Day 8). Increasing only the early flowers to raise the total flower number to 88 (the unmodified file contained 48 flowers) almost doubled fruit number when ASMAX = 0 and 300 mg glucose equivalents (Fig. 7). Increasing only the late flowers had essentially no effect on fruit number.

Assimilate utilization early in the fruit set period is low because most fruits are still in the lag phase of growth, so there is usually more than enough assimilate to allow early fruits to reach the end of SEN without aborting. Consequently, increasing the number of early flowers increased the number of fruits. Adding late-developing flowers had little effect on fruit number (Fig. 7). The extra late-developing fruits apparently aborted because the early fruits were growing rapidly during the initial growth of the late fruits and used most of the available assimilate. These results from SOYPOD are consistent with observations that early fruits at a raceme survive at much higher levels than late fruits (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986a; Nakamoto et al., 2001; Egli and Bruening, 2002a) and that increasing early flowers experimentally significantly increased fruit number (Egli and Bruening, 2002b).

### Short-Term Variation in Photosynthesis

Although the link between photosynthesis and fruit and seed number is well established, less is known about the effect of short-term variation in photosynthesis on fruit survival at individual nodes. Most published studies compare average or total photosynthesis during flowering and fruit set with fruits and seeds at maturity (Ramseur et al., 1985; Egli and Zhenwen, 1991; Bruening and Egli, 1999). Therefore, I evaluated the effect of short-term variation in photosynthesis on fruits per node by increasing or decreasing relative photosynthesis in SOYPOD from 0.05 to 1.0 or from 1.0 to 0.05 for 1-wk intervals during the flowering period with ASMAX set at 300 mg glucose equivalents (Fig. 8). The only effect of a single

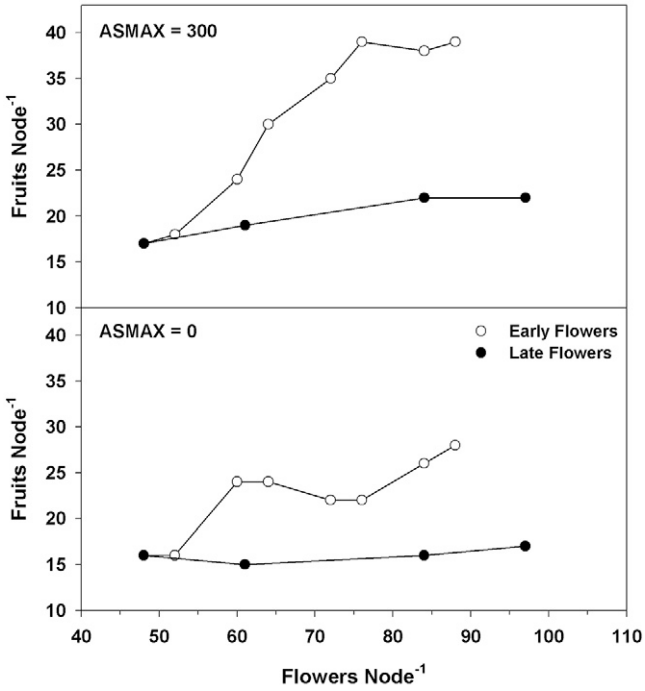


**Fig. 7. The effect of increasing flower production on fruit number. The flowers in the input file (Fig. 2) were multiplied by a factor >1 to increase flower number while maintaining the original temporal distribution. The unmodified file contained 48 flowers. "Early" refers to the flowers produced on the main raceme from Day 1 to Day 8 (Fig. 2). "Late" refers to the flowers produced after Day 8 and represents flowers produced on sub-branches. SEN was set at 25, ABRTM at 16, seed growth rate at 6.20 mg seed$^{-1}$ d$^{-1}$, and relative photosynthesis at 1.0. Flower and photosynthesis data are from the one girdled-node treatment of Experiment 2 from Egli and Bruening (2002a).**

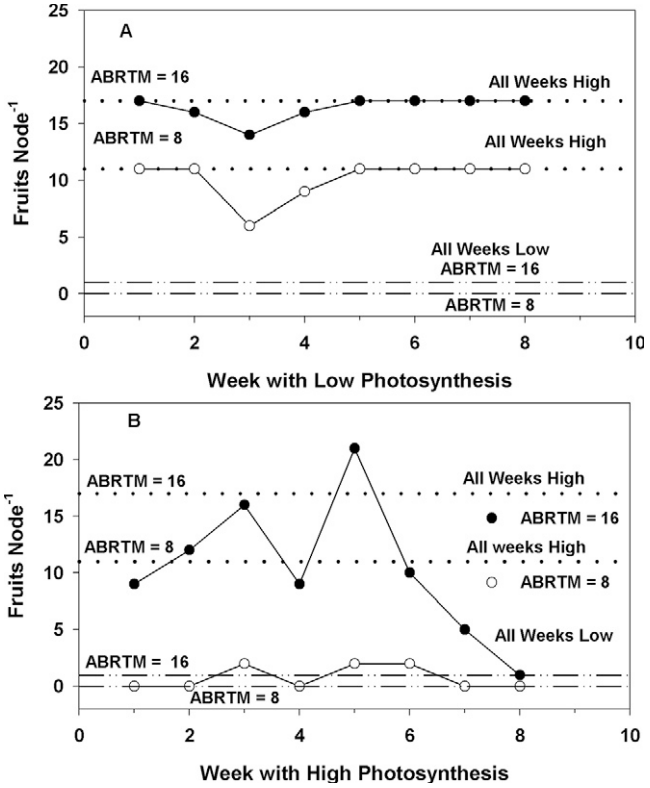


**Fig. 8. Effect of 1 wk of (A) low (relative photosynthesis = 0.05) or (B) high (relative photosynthesis = 1.0) photosynthesis in SOYPOD on fruits node$^{-1}$ for ABRTM = 8 or 16 d. Input data from the one girdled-node treatment of Experiment 2 are from Egli and Bruening (2002a), with SEN = 25 d, ABRTM = 8 or 16 d, seed growth rate = 6.20 mg seed$^{-1}$ d$^{-1}$, and ASMAX = 300 mg glucose equivalents. The high or low photosynthesis treatment was applied for 1 wk during the flowering period with photosynthesis set at the alternative level for all other weeks. All fruits had set or aborted by the end of Week 8.**

week of low photosynthesis was a reduction in fruits per node during Weeks 2, 3, and 4 (Fig. 8A). The maximum reduction was larger for ABRTM = 8 d (50%) than for ABRTM = 16 d (21%). Providing the model with only 1 wk of high photosynthesis with ABRTM = 16 d increased fruits/node in all weeks except Week 8 (Fig. 8B), with the largest effect occurring in Week 5. The week of high photosynthesis had very little effect on fruit number when ABRTM was shortened to 8 d. Reducing ASMAX to 0 reduced maximum fruits per node (i.e., with all weeks at high photosynthesis), but the patterns for 1 wk of high photosynthesis were essentially the same as ASMAX = 300 mg glucose equivalents (data not shown). The fluctuations associated with 1 wk of low photosynthesis were almost nonexistent with ASMAX = 0.

The greater sensitivity of fruit set to a week of high photosynthesis than to a week of low photosynthesis probably relates to the requirement that a fruit must experience ABRTM consecutive days of assimilate deprivation before it aborts. A week of low photosynthesis would trigger abortion only if the fruit had already accumulated enough days of assimilate deprivation so that an additional week would satisfy ABRTM. This scenario was relatively rare but was more common for ABRTM = 8 than for 16 d (Fig. 8A). High photosynthesis for a week or even a single day can restart the ABRTM counter and greatly increase the chances that the fruit will reach the end of SEN before it reaches ABRTM, resulting in survival. Thus, the effect of a week of high photosynthesis is magnified with the peak response for ABRTM = 16 d occurring later during flowering when there were more fruits that could benefit from restarting ABRTM. The maximum response represented a 20-fold increase in fruits node$^{-1}$. A week of high photosynthesis had little effect when ABRTM = 8 d (with SEN = 25 d) because there was still ample time after ABRTM was reset for the fruit to reach ABRTM and abort before it reached SEN.

These results suggest that the fruit set process acts to maximize fruit number in a given environment by taking advantage of short periods of highly productive environmental conditions while being relatively tolerant of short periods of poor environmental conditions. These results must be interpreted with at least two caveats. First, changes in photosynthesis in SOYPOD are immediately translated into changes in the supply of assimilate to the fruits. This may not occur in planta where the supply may be buffered by storage carbohydrates in a manner not mimicked by SOYPOD. Second, SOYPOD represents only a single node, whereas yield is produced by a community made up of individual plants, each comprising a collection of individual nodes. We cannot assume that the community will mimic the response at a single isolated node.

## SUMMARY

The number of fruits and seeds produced by soybean plants have long been linked to photosynthesis and the availability of assimilate. The SOYPOD model combines this approach with the dynamics of flower production and the characteristics of the developing seed to predict fruit set at an isolated node. This model accurately mimicked the characteristics of fruit set in field and greenhouse experiments, suggesting that the rules embedded in SOYPOD provide a reasonable first approximation of the mechanisms involved in determining fruit and seed number in soybean. The model corroborates the dependence of fruit number on the temporal distribution of flower production and seed characteristics identified experimentally. The model also suggests that the plant can take advantage of short periods of high photosynthesis and tolerates short periods of low photosynthesis—an ideal arrangement for maximizing fruit number. If SOYPOD accurately represents isolated nodes, it could serve as the basis for a whole plant–plant community model, with repeated SOYPOD units representing the individual nodes that make up the plant and the community. Constructing a whole-plant model requires simulating the assimilate supply by node and dealing with assimilate transfer and potential interactions between and among nodes, introducing another layer of complexity into the model. The potential gains in our understanding of the yield production process that would come from such a model probably make dealing with the extra complexity worthwhile.

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