REALISATION OF YIELD POTENTIAL IN SOYABEAN
GLYCINE MAX (L.) MERR. AND COWPEA
VIGNA UNGUICULATA (L.) WALP.

R. J. Summerfield, F. R. Minchin and E. H. Roberts

University of Reading, Department of Agriculture and Horticulture, Plant
Environment Laboratory, Shinfield Grange, Shinfield, Reading RG2 9AD

Summary Whilst average yields of many cereal grains have increased drama-
tically over the last 25 years, those of the major grain legumes have
either stagnated or have declined.   When the economic yield of a crop is
poor despite successive efforts to improve it we must surely question the
rationale and strategy which have been previously adopted.   Almost every
sphere of physiological interest in legume crop improvement is rife with
confusion, contradiction, inconsistency and erroneous interpretation often
based on unreliable methodology.   Not surprisingly, despite many attempts
over the last 20 years to improve yields in soyabeans by applying growth
regulators, none are commonly used in commercial practice.   Indeed, selec-
tion criteria for the evaluation of chemicals with potential 'growth regu-
lating activity' have not been satisfactorily developed.   The reasons for
this situation and the future possibilities of escaping from it are dis-
cussed.

INTRODUCTION

Soyabeans (Glycine max (L.) Merr.), about two thirds of which derive from USA
crops, account for more than half the total global production of major grain legumes.
Cowpea (Vigna unguiculata (L.) Walp.) production data appear less frequently in world
statistics, but recent figures indicate a total world production equivalent to just
2.4% of the soyabean output, with more than 95% of this coming from Africa (calcula-
ted from 38).   Soyabeans are most often grown in pure stands and with sophisticated
agronomic inputs whereas cowpeas are a traditional component of mixed cropping and
seldom benefit from weed control, crop protection or irrigation.   An annual rotation
of soyabeans and maize is common practice in the USA whereas cowpeas are usually
planted soon after staples such as sorghum, maize or millet and will grow and mature
during the same season (28, 34).

After more than fifty years of research, development and commercial production
of soyabeans in the USA (during which time the average yields of many cereal grains
have increased by 50-100%) current average yields are little better than those re-
corded in 1950.   From a detailed survey of the literature we have calculated that
average farm yields of USA soyabean crops have increased by 14-21% over the last 30
years.   The current national average stands somewhere between 1750 and 4000 kg/ha,
although the majority of sources quote values around 2000 kg/ha.   Not surprisingly,
reports of investigations attempting to 'break the soyabean yield barrier' are in-
creasingly common in the scientific literature.   Toward this end, the effects of
numerous chemicals with potential 'growth regulating activity' have been evaluated
over the past twenty years and yet there are no compounds commonly used in current
commercial soyabean production (9).   Then again, maximum farm yields up to four
times the national average have been reported (eg 7).   The reasons for these 'con-
test-winning' yields have not been defined but, clearly, the 'yield-barrier' is not
beyond penetration!

Adjacent farms commonly produce soyabean yields differing by 25-50%.   This is
primarily due to (mis)management (29).   For example, there is considerable evidence

that seed yield is principally a function of seed number produced (eg 51) except where crops are subjected to physiological stress, delayed planting or where a large proportion of the yield is derived from branch nodes (35). However, variations from field-to-field and year-to-year in average seed size of a given variety commonly range up to 60% (13)!

The realisation of less than a decade of intense, co-ordinated research on cowpea has yet to be reflected in world production figures. It is perhaps surprising then that the application of growth regulators to increase yields is already seen by some as a worthwhile component of crop improvement strategies (eg 37). In marked contrast to soyabean, little is known of the variation in cowpea seed yields from farmers crops in Africa. The only safe generalisation is that average yields are small, probably between 100 and 300 kg/ha, and total crop failures are not uncommon (32). However, experimental yields are commonly between 1000 and 2000 kg/ha when improved, determinate cultivars are grown under improved management conditions, and often exceed 2,500 kg/ha with multiple harvests from indeterminate types (17).

Clearly, these two species are at different stages of development in terms of crop improvement, and thus the factors limiting yield may also be quite different. Yet we have a situation in which strategies for the improvement of soyabean yields are being applied somewhat uncritically to the improvement of cowpeas. We believe that a comparison of the physiological yield-limiting processes in both crops should lead to a more rational strategy for their improvement, and even for the improvement of legumes in general.
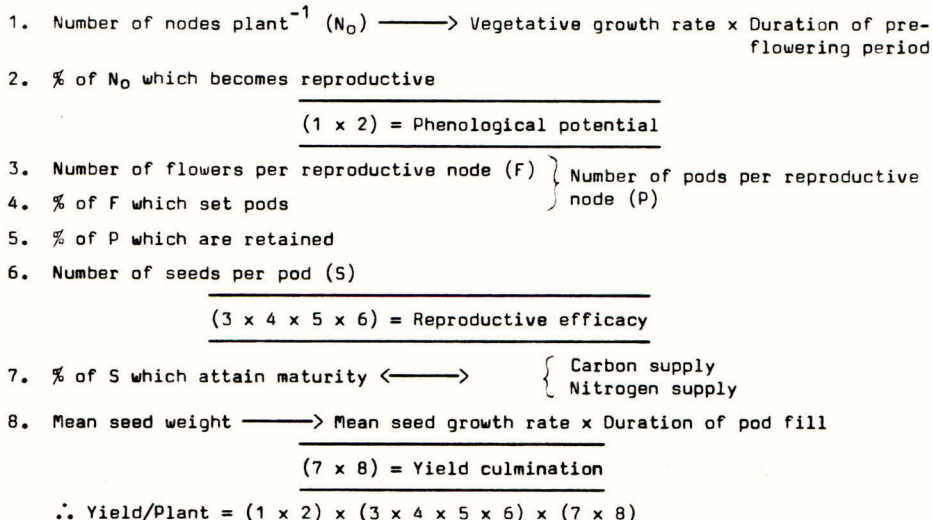

ADAPTATION TO ENVIRONMENT

Phenotypic variation in most crop plants is the consequence of a combination of genetic differences, the effects of environment on growth and reproductive development and of genotype x environment (GE) interactions. However, this combination of factors is likely to provide an inadequate, and even misleading, description of phenotypic variation in a legume crop because it does not consider the Rhizobium genotype upon which plants may be largely dependent for their nitrogen supply, or the likelihood of Rhizobium x host or Rhizobium x environment, or indeed second order interactions. Unfortunately, there are so many examples, especially with soyabeans, where the relationships with Rhizobium have been ignored that to attempt to list them would be unnecessarily time-consuming and depressing. A recent example involved the testing of numerous soyabean genotypes in two locations in different years (2). The authors concluded that 'Diverse weather patterns between years were ideal for studying GE in soyabeans' and, without reference to any aspect of nitrogen nutrition, 'Single environment preliminary yield tests can be used without serious risk of discarding outstanding lines'!

Our understanding of environmental adaptation in all grain legumes has been influenced in no small way by the discovery more than 50 years ago that photoperiod had a marked effect on floral induction in soyabeans. Indeed, genotypic variation in response to photoperiod has formed the basis of a commercial system of soyabean maturity groups in the USA. Early maturing, indeterminate types with an 'optimum daylength' for flowering of about 16 h are grown in the northern states and Canada whereas later maturing, determinate types with an 'optimum daylength' of around 14 h are customarily grown in the extreme south (50). The effects of daylength and temperature are so marked and specific that most American varieties are generally restricted to within 4° latitude (480 km) of their 'adapted area'. Outside this range plants either fail to mature before frost in the north or flower and mature too early in the south (22). The effects of other environmental factors, and especially of their interactions with daylength, on growth and development have been seriously neglected despite observations made 40 years ago that cool temperatures, particularly at night, can modify the response of soyabeans to inductive photoperiods (41). Beyond doubt, the standard maturity group classification can lead to considerable errors when predicting varietal adaptability (19). Furthermore,

regression models which relate reproductive development to changes in daylength and average daily temperature (eg 23) are seriously inadequate when applied to low latitudes outside the areas for which they were generated. Then again, simulated responses using a computer model to just a 2°C decrease in 'normal air temperatures' under 'normal precipitation conditions' varied from a 92% reduction to a 17% increase in yield over a four year period at a single locality (4). Undoubtedly, such dramatic consequences simply reflect the many erroneous assumptions and over-simplifications inherent in this model.

Seed yields in both soyabean and cowpea are dependent upon the product of both vegetative and reproductive components (Fig. 1) which themselves are markedly affected by environmental factors. There is an urgent need for quantitative data on each of these components and the consequent variations in seed yield when plants are grown in contrasting environments. Only then can the main effects and interactions of climatic factors on the more responsive components contributing to significant variations in yield be identified with confidence. Researchers can then seek to improve these components genetically or even through a far more rational selection of growth regulating compounds than has previously been possible. For example, after a series of experiments investigating under controlled environment conditions the effects of factorial combinations of daylength, day and night temperature on growth and reproductive development in soyabean and cowpea under conditions of carefully regulated nitrogen nutrition, we have devised a scheme for predicting relative seed yield over a range of humid tropical conditions (43). For the range of each climatic factor so far investigated, the environmental control of vegetative growth and reproductive ontogeny in both species is largely dependent on differences in, and interactions between, daylength and night temperature and genotypic sensitivity to each factor with respect to the onset of flowering. Furthermore, for both species, genotypes may come into first flower in almost exactly the same time in different daylengths depending upon whether the nights are warm or cool. These findings highlight just how easily erroneous conclusions could be drawn from time-of-planting experiments in the field, or when independent day and night temperature controls are neglected in controlled environment studies. An example of such an erroneous conclusion is that 'temperature effects on flowering /in soyabean/ are apparent in the field only when the effects of daylength are negligible' (20).

Fig. 1   Components of seed yield in determinate soyabeans and cowpeas (from 44)

1. Number of nodes plant^{-1} (N_O) ——————> Vegetative growth rate x Duration of pre-
                                                                    flowering period

2. % of N_O which becomes reproductive
    _____
                      (1 x 2) = Phenological potential

3. Number of flowers per reproductive node (F) ⎫ Number of pods per reproductive
                                                                   ⎬ node (P)
4. % of F which set pods   ⎭

5. % of P which are retained

6. Number of seeds per pod (S)
    _____
                    (3 x 4 x 5 x 6) = Reproductive efficacy

7. % of S which attain maturity <———————> ⎧ Carbon supply
                                                            ⎩ Nitrogen supply

8. Mean seed weight ————> Mean seed growth rate x Duration of pod fill
    _____
                        (7 x 8) = Yield culmination

    ∴ Yield/Plant = (1 x 2) x (3 x 4 x 5 x 6) x (7 x 8)
    _____

The effect of night temperature on time-to-flowering in soyabean has been cor-
roborated under cooler temperature conditions by Tanner and Hume (48) who found that
cultivars adapted to more northerly latitudes were more affected by cool days than
later-maturing genotypes which were more sensitive to cool nights.   These findings
raise serious questions on the north-south adaptation of supposedly 'photoperiodic-
insensitive' cultivars when in many cases the effects of temperature on flowering
have been ignored.

Using the same daylength (12 h) as Tanner and co-workers, we have not detected
any significant effect of warmer day temperatures ($27°$-$33°C$) on time-to-flowering in
either soyabean (8 cultivars) or cowpea (52 cultivars).   Clearly, we urgently need
to know the shape of response surfaces for daylength and temperature effects on
flowering in both legumes.   In the interim, we contend that the use of supposedly
'day-neutral' genotypes as parents in a breeding programme (30) for developing broad
geographical adaptability is an unreliable strategy.   Then again, the use of such
cultivars is not a reliable basis for producing 'standard' plant material in poorly
controlled environments for the year-round evaluation of growth regulating compounds.

Not only can flower development (<u>cf</u> induction) and pod set be more demanding in
their daylength requirements than is flower initiation - at least in photoperiodical-
ly responsive soyabeans and some Nigerian cowpeas (10, 53) - but also reproductive
efficacy and yield culmination (see Fig. 1) are very dependent on air temperatures,
especially during the day, under which the crop matures (eg 24).

Under simulated tropical conditions (see below) it is only after flowering when
a marked effect of day temperature is detected and then an increase of no more than
$6°C$ (maintained throughout the life of the plant) can have a drastic effect on ulti-
mate seed yield.   By promoting rates of leaf and nodule senescence, increasing
flower and pod abscission and shortening the duration of reproductive growth, warm
($33°C$) as compared with cooler ($27°C$) day temperatures commonly reduce the yield of
both species by 50% or more.   Genotypic differences in sensitivity to warm days
during the later stages of reproductive ontogeny may well dictate the outcome of
phenological potential for seed production (Fig. 1), whether or not this has been
maximized by appropriate selection for daylength and temperature effects during vege-
tative growth.   Accordingly, we have devised and tested the reliability of an inte-
grated field-glasshouse screening strategy for cowpeas and potentially tropic-adapted
soyabeans (45).   Cultivars identified as 'daylength-insensitive' (or 'sensitive') in
the field are then screened for day and night temperature effects on the onset of
flowering and seed yield under carefully controlled conditions in a glasshouse.
When the direction, magnitude and interacting effects of climatic factors on selected
varieties are known, the types needed for particular circumstances can be more criti-
cally defined and potential sources of genetically-adapted or invariant material can
be identified.

PLANT CULTURE IN CONTROLLED ENVIRONMENTS

Because in the natural environment daylength and temperature tend to be highly
correlated, and there are marked variations in temperature with altitude as well as
latitude, controlled environments can be a powerful adjunct to field research on en-
vironmental adaptation in grain legumes (eg 42).   Furthermore, preliminary trials
for evaluating new chemicals of unknown biological activity are invariably carried
out in growth rooms or in glasshouses.   Even though a well-designed trial will often
produce data requiring only a minimum of formal statistical analysis, the results
may have little relevance if test cultivars do not closely resemble plants grown in
the field.   Most soyabean research workers have apparently assumed they knew how to
grow plants in controlled environments but the findings of Tanner and Hume (48), who
have recently surveyed 30 major soyabean research centres in the USA, are obvious
testament to the fact that this assumption was wrong.   They discovered that the
most common problem was an inability to produce a 'typical' field-grown plant because
of etiolation, abnormal branching and leaf expansion.   However, we have now

developed and tested a whole range of plant husbandry techniques which take the
widest possible viewpoint of the legume-Rhizobium symbiosis (46).   With an appro-
priate selection of practices for each species the field phenotype can be closely
imitated under controlled environment conditions (eg for cowpea see Table 1).
Recent publications have advocated the standardization of controlled environment re-
search in terms of the basic information on plant culture which should be reported
(eg 1).   It is hoped that these objectives can now be achieved in experiments with
grain legumes so that differences in plant growth (eg stem elongation, branching and
leaf expansion), which cumulatively influence seed yield, can be ascribed with con-
fidence to the experimental treatments imposed.

Table   1

Selected morphological attributes of cowpea cv TVu 4552 grown in the field at Ibadan,
Nigeria and in controlled environment growth cabinets (see 47 for details)

Location	Days to first flower	Plant height (cm)	No./plant of Branches	No./plant of Main stem nodes	Terminal leaflet Length (cm)	Terminal leaflet Width (cm)
Field	38	53	3.5	12.4	13.5	10.2
Cabinet a)	37	62	3.3	10.3	12.0	8.5
b)	37	52	3.3	10.0	12.0	8.5

(a) and (b) denote different lamp combinations

NITROGEN NUTRITION, CARBON METABOLISM AND YIELD

Reasonably reliable estimates from properly conducted field trials in tropical
and sub-tropical locations have shown an average symbiotic N_2 fixation in soyabeans
of 103 kg N/ha/annum (range 1-168 kg) compared with 198 kg N/ha/annum (range 73-354
kg) in cowpeas (27).   However, under farmers' conditions in the USA the 4-year
average fixation by these crops is only 88 and 25 kg/ha/annum, respectively (27).
Since all commercially-grown soyabeans in the USA can be traced back to 6 plant in-
troductions from the same area of China (29), it may not be unreasonable to suspect
an underlying genetic limitation to symbiotic performance.   However, cowpeas suffer
even more dramatically under similar agronomic conditions, which implies that farming
practices in the USA may, too, contribute significantly to the limited realisation of
legume symbiotic potential.   In Brazil, the worlds second largest producer of soya-
beans, many varieties from the USA form relatively few nodules and are capable of
satisfactory symbiosis only under 'optimum' soil and environmental conditions, and
with specific strains of Rhizobium (6).   This is hardly surprising since most bree-
ding programmes neglect nodulating ability completely and new cultivars are selected
in plots heavily fertilized with mineral nitrogen.   Soyabean nodules contribute only
about 50% of total plant N when crops are grown without any applied mineral nitrogen
(18), and values are typically closer to 25% (14).   Clearly, the extensive varia-
bility in legume symbiosis promises great scope for improvement - even in soyabeans
(and see 26).

Compared with cowpeas, which have only recently received detailed attention, the
literature on interrelationships between carbon metabolism and nitrogen nutrition in
soyabeans is both legion and confusing.   Different investigators report symbiotic
activities at similar stages of growth which differ by an order of magnitude, or more
(compare 3 with 16);   others have adopted techniques long known to reduce nodule ac-
tivity (as measured by the reduction of acetylene to ethylene) by up to 75% (eg
washed root samples; 49), and many have failed to regulate assay temperature and the
time during each diurnal period when samples are taken or have used an inappropriate
C_2H_2/N_2 conversion ratio (see the excellent treatise in 12).   Notwithstanding these
problems, we can be certain that the availability to nodules of recently-formed

carbohydrate from shoot photosynthesis is a major factor regulating the rate of sym-
biotic nitrogen fixation (see 14).

In many soyabean crops, nitrogen fixation makes little contribution to the
plants' N status for periods up to 50-60 days after sowing, peak values are recorded
'somewhere near the end of flowering' and symbiotic performance declines precipitous-
ly during pod-fill (eg 39).   The popular hypothesis is that seed yields are limited
because photosynthate supplies are monopolised by rapidly developing fruits thus re-
ducing carbohydrate supply to nodules and hence symbiotic fixation.   Nitrate uptake
and nitrate reductase activity have also declined markedly by this stage (16), hence
foliar N compounds are mobilized to fruits and this reduces photosynthesis rate,
hastens senescence and the plants prematurely 'self-destruct' (36).

Seasonal patterns of nitrogen fixation for more and less efficient soyabean-
Rhizobium association differ markedly (52).   We have compared these seasonal changes
with those described by Brun and co-workers who interpreted their data to show that
'activity decline in the nodules is caused by a competition for available photosyn-
thates from the developing pod sink' (3).   These data were selected for comparison
since the different crops had similar vegetative periods, crop durations and peak
nodule fresh weights (about 80 days from sowing to the end of flowering, 120 days
from sowing to maturity and 4-5 g nodule fresh weight/plant, respectively).

Despite the incorporation of 11,200 kg/ha organic matter into the soil before
sowing in an attempt to immobilize inorganic N, only meagre nodulation and symbiotic
activity were recorded for the first 50 days of vegetative growth in cvs Clay and
Chippewa (3).   Weber et al. (52) did not apply such treatments and also recorded a
similar 'lag' phase but neither group of workers measured available soil N content!
All cultivars showed markedly different relationships between seasonal fixation pro-
file, nodule weight and dry matter yield of 'tops' and/or pods.

There is obvious variation as to the effects of flowering on nodule function
and longevity of bacteroid tissue.   Indeed, other studies have provided data which
fail to corroborate the 'popular' hypothesis since fixation rates remained at near-
maximum values throughout reproductive growth (15, 21), or even increased during the
rapid pod-fill stage (5).   Then again, none of the estimates of symbiotic fixation
have been made on high yielding (> 4000 kg/ha) crops and if, as Shibles et al. (35)
so cogently argue, potential yield is determined largely by events prior to seed
filling (see Fig. 1), what is the consequence of poor fixation and/or N uptake during
early development?   Under tropical conditions, cowpeas can accumulate between 43
and 50% of their total N during a 35 day vegetative period compared with an accumu-
lation of just 25% during a similar period in soyabeans (31).   Even though each crop
produced an equivalent nodule mass, peak efficiencies in soyabean were only 20% of
those in cowpea.   Accordingly, soyabeans accumulated 31% less total N during a 70
day crop duration but that in seeds represented 80% of the total compared with 60%
in cowpea.   The rate of pod development in soyabeans is much slower (30-52 days to
maximum seed dry weight depending upon temperature) than in cowpea (18-23 days) and
this presumably reduces the rate of N uptake into fruits and so contributes to de-
layed senescence.   We still have little idea of the daily needs of an individual
fruit from its parent plant!   Foliar fertilization with solutions containing N, P,
K and S in proportions similar to those found in seeds was reported to produce high-
ly significant responses in soyabeans (due to increases in seed number but not seed
size) when applied during seed filling (11), but others have failed to repeat this
success (eg 31).   However, the original report makes no mention of spraying control
plants with water plus surfactant and, since the experiments were carried out during
two years when unusually hot and/or dry weather restricted plant growth and develop-
ment, it is not clear whether the treatment effects were due to mineral nutrition
or overcoming a water deficit.   In any case, the circumstances seemed exceptional
in other ways since on both occasions excessive rainfall delayed planting and in one
year early frost arrested seed development!

A series of experiments have clearly shown a genetic potential in cowpea for
very large seed yields from symbiotic associations dependent on fixed nitrogen (25).

Under close-to-optimum temperature conditions, spaced plants inoculated with a single strain of Rhizobium (CB 756) can produce about 100 g dry weight of seeds in 90 days from sowing and throughout growth derive between 85 and 93% of their total requirements from fixation (8). Furthermore, as for plant morphology (Table 1), the proportion of total plant N in seeds and contributions to this from various sources are remarkably similar for plants grown in the field and under controlled environment conditions (8; and see 31). We know of no data where these types of comparisons have been made in soyabean.

Nodule-dependent plants are potentially no less environmentally adaptable than those relying on inorganic N, and they produce equally or even better seed yields (25). Plants receiving 20 ppm N obtain at least 85% of their total N requirements from fixation (8) whereas in those irrigated with 200 ppm N symbiotic activity is almost completely suppressed. Other strains of Rhizobium isolated from tropical soils have provided N sufficient for even greater yields (up to 147 g/plant) and can be inhibited by even small amounts (30 ppm) of inorganic N. For symbiotic combinations so far investigated, fixation in soyabeans is generally less efficient than in cowpeas because an average of 30% of the energy utilized in symbiotic activity is wasted on hydrogen evolution rather than being involved in nitrogen fixation whereas only about 5% is lost in this manner in cowpeas (33).

Just as a breeding objective such as increased net photosynthesis rate may be irrelevant unless the reproductive behaviour of the legume crop is well adapted to the local environment (10), so is the evaluation of growth regulators to try and arrest 'self-destruction' when the role of the microsymbiont in the realisation of yield potential is ignored. Apart from major differences between soyabeans and cowpeas, fixation profiles (initiation, incremental rates, duration of peak fixation and total N fixed during growth) are markedly different between both determinate and indeterminate types and early and late maturing varieties (15). Until the reasons for these differences are known there seems little chance of exploiting them, either through appropriate management practices or the selection of genotypes with greater symbiotic potential, or indeed by applying growth regulators.

PROSPECT

Almost every sphere of physiological interest in legume crop improvement is rife with confusion, contradiction, inconsistency and erroneous interpretation often based on unreliable methodology. Soyabeans seem to have suffered surprisingly severely in these respects since they have been for so long the world's most economically important grain legume and therefore subject to a great deal of investigation. With the benefit of hindsight we believe that similar mistakes can be avoided in cowpea. Furthermore, we believe that several major aspects have been overlooked in previous attempts to identify yield-limiting processes in grain legumes. These ideas are under investigation at Reading in a collaborative project with IITA (Nigeria) and can be briefly summarized viz:

1. Experiments on cowpea (and Pisum) have shown that peak fixation values coincide with a 'switch-over' from the host plant being largely dependent on older nodules located on, or near, the tap root, to relying on a younger, more efficient, nodule population located on secondary and higher order lateral roots. Furthermore, if soyabean and cowpea plants are kept vegetative, fixation activity shows no tendency to 'peak' when plants reach the age at which they would normally flower. We contend that these data could be interpreted to show that during the period between floral initiation and anthesis nodulated plants respond to a hormonal 'trigger' and boost their symbiotic activity. Should we therefore regard the onset of reproductive growth as a stimulant or depressant of nodule performance?

2. To maximize dry matter accumulation in seeds not only must leaf senescence be delayed so as to prolong photosynthesis but also nitrogenous compounds (including ureides such as alantoic acid) must be fluxed rapidly from leaves to fruits. Our current, albeit limited, data suggest the chances of achieving and improving this

dual foliar role in seed production are greater when plants rely on symbiotic rather than on inorganic nitrogen.

3. Although the essential role of photosynthate supply in nodule functioning is well documented, the regulatory mechanism per se is not fully understood. An assumption, not generally challenged, is that nodules are responsible for metabolizing all the carbohydrate for their own maintenance and growth and for generating energy for N_2 fixation and organic acid skeletons for amino acid production. However, roots of nodulated legumes can have very high respiration rates hence may they not be a site for some aspect of the carbohydrate metabolism associated with N_2 fixation?

4. Indirect evidence for the limiting effect of photosynthate supply on N_2 fixation has been proposed from studies on diurnal fixation patterns. However, detailed examination of published data suggests that the host's transpiration rate could equally well be a major controlling factor - mediating the removal of fixation products from the nodules, and possibly also affecting the rate of water supply to them.

5. During both vegetative and reproductive growth the overall metabolic activity of the nodule population must be regulated so as to maximize, but not to prejudice, growth of the host plant. Nodules are known to produce large quantities of auxins, cytokinins, gibberellins and abscissic acid but the role of phytohormonal interactions between micro- and macrosymbiont are almost completely unknown.

In general, 95% of incident radiation is intercepted by soyabean and cowpea crops when LAI ranges from 3 to 4 and leaf photosynthesis rates in both species are then normally between 20 and 30 mg $CO_2/dm^2/h$ (38). It is not uncommon for both legumes to abort more than 50% of the flowers which reach anthesis, especially under hot and/or dry conditions and, subsequently, young pods seem especially sensitive to environmental stress. In some legumes, nitrogen fixation appears more sensitive to water stress than either the uptake and utilization of inorganic N or carbon fixation (40). The main amino acid exported from soyabean nodules is asparagine whereas in cowpea it is glutamine. The former nodules are spherical with well-developed lenticels whereas the latter seldom have such obvious surface features. Related to nodule morphology is the fact that soyabeans are more sensitive to water stress than are cowpeas but are better equipped to tolerate waterlogged conditions. Basic similarities and major differences thus contribute to yield potential in each species (apart from the genotypic variations within species) and our knowledge of them is, in general, rudimentary. However, progress is already hampered by ill-founded dogma. All concerned with yield improvement in grain legumes must recognize and accept this situation before significant improvements can be made through manipulating physiological limitations to yield, either by conventional plant breeding or applying chemical compounds.

Without doubt, in the vast majority of cases, the most effective way to obtain a phenological pattern which is most efficient in a given environment for a specific purpose (eg seed production) is to breed an appropriate genotype! Historically, plant breeders have used economic yield itself as a measure of progress but a detailed knowledge of the components of yield (eg see Fig. 1) can permit a more rational strategy for improving individual limiting factors. The most challenging aim in developing synthetic growth regulations is, arguably, to discover compounds which can overcome these limiting steps in developmental physiology by modifying the biosynthesis and/or translocation of endogenous hormones or by interfering at their sites of action. Then again, since large numbers of genotypes and chemicals (with appropriate controls) cannot be screened in a crop situation, a reliable and predictive screen or bioassay must also be developed. Irrespective of the scale, practicality, climatic effects and vagaries of weather which will all impinge on attempts to regulate crop growth by chemical means, or the contributions of micro- and macrosymbiont to phenotypic variation among progenies in a legume breeding programme, we cannot hope to make significant progress (other than by improved crop protection and management) in legume yield improvement without much more detailed knowledge of the developmental physiology of the symbiotic system.

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DEVELOPMENTAL PARAMETERS REGULATING SUGAR YIELD IN BEET

G. F. J. Milford and J. R. Lenton

Rothamsted Experimental Station, Harpenden, Herts. AL5 2JQ

INTRODUCTION

In many field crops growth rate and final yield are directly rela-
ted to the amount of radiation intercepted. The few measurements that
have been made with sugar beet suggest that it behaves similarly when
its growing season is altered either by varying the sowing date or by
shading the crop in contrasting seasons (1,2). The implication is
that sugar yield can be increased by improving the interception and
efficient use of radiation to produce harvestable sugar. In this
paper we attempt to define certain developmental and physiological fac-
tors specific to sugar beet which affect these two processes and
suggest likely ways in which they might be beneficially modified by
plant growth regulators. We shall not consider hormonal control or
modification of such fundamental processes as photosynthesis, respira-
tion, or the means by which changes in the rate and direction of trans-
location affect the partition of assimilate as these will be considered
in detail in other papers in the sesson.

PROCESSES AFFECTING RADIATION INTERCEPTION

a) Crop establishment. Much of the current sugar-beet acreage is
drilled to a stand using pelleted monogerm varieties. This, together
with the trend toward wider spacing and minimum handwork, underlines
the requirement for seed of good quality to give maximum germination
under field conditions so as to establish an early, uniform and vigor-
ous crop. Sugar beet is naturally biennial, requiring an over-
wintering period of vernalisation before flower induction, stem

elongation and seed production on the indeterminate inflorescence during the second year. Environmental conditions experienced by the mother crop are known to influence seed progeny performance. For instance, low rainfall or low temperature during seed development causes poor germination and predisposes the subsequent crop to bolt during the first vegetative season (3,4). Growth inhibitors present in the maternal tissue surrounding the seed may be partly responsible for poor germination (5), but attempts to improve seed performance by pretreatment with aqueous solutions of growth promoters seem to have encouraged germination more by leaching the inhibitors than by direct stimulation of the embryo (6).

Within a given seed lot the large, mature seeds in those fruits produced early on the main branches of the inflorescence show greater percentage and rate of germination and produce more vigorous seedlings giving greater sugar yields than the underdeveloped seed produced later (7,8). A considerable effort is required to rub and grade sugar-beet seed and between 70-90% of the seed crop is discarded during commercial grading (9). Chemical modification of the seed crop to produce a smaller, more determinate inflorescence should reduce the cost of seed processing and produce an earlier and more easily harvested seed crop with much improved performance characteristics. So far, attempts to achieve this with currently available growth retardants have not been particularly successful (10).

b)   Canopy development. The sugar-beet crop intercepts only 60% of the incident radiation during a normal growing season in Britain. Seed is sown at relatively wide spacing and the crop is slow to establish full leaf cover which is usually incomplete during June and July when incident radiation is greatest (1,11). Agronomic treatments, designed to accelerate early leaf cover, such as additional nitrogen fertiliser or closer planting, usually improve total dry matter production but the increase in sugar yield is often less because much of the extra dry matter produced is retained in the shoot (12). Cold temperatures in Spring are thought to be the major environmental factor limiting early season leaf growth. Studies in controlled environments show that low temperatures reduce the rate of leaf production and expansion and decrease the maximum potential size of the individual leaves (13,14). Night temperatures may be more important than day temperatures in controlling leaf expansion in sugar beet as detailed diurnal measurements show that the rate of leaf expansion is much greater during periods of low

irradiance and darkness than in high-intensity light (15).   The detri-
mental effects of early-season low temperature on final sugar yields
can be avoided to some extent by transplanting established seedlings
but at present this method is uneconomic in Europe although widely used
in Japan (16,17).

Experiments in controlled environments have established that light
quality and duration affect leaf growth independently of temperature.
Extending the daylength with low-intensity tungsten light, rich in
energy from the red and far-red wavelengths, causes marked increases
in leaf area and petiole growth (18).   These photomorphogenic respon-
ses to differences in light quality at the end of the day are relevant
to the growth of the crop in the field as it is exposed to similar con-
ditions in the natural environment (19).   The crop canopy can also
modulate the spectral energy distribution of incoming radiation toward
the far-red wavelengths as it is transmitted down the leaf profile (20).
Short exposures to far-red light increase petiole growth and could be
one of the factors stimulating shoot growth in densely spaced crops
(21).   The demonstration of a photoperiodic change in leaf develop-
ment is also important in that it shows that leaves of current commer-
cial genotypes possess a much greater potential for expansion than they
usually exhibit in the natural environment. We have circumstantial
evidence that the photoperiodic responses are controlled in part by
changes in endogenous growth substances, particularly the gibberellins
(22).   Theoretically, it should be possible to substitute the light
stimulus for leaf expansion by applied growth regulators; we believe
this might be a rational and potentially attractive approach to accel-
erating early season leaf growth.

The amount of radiation intercepted by the crop during growth is
increased when the season is extended by early sowing or late harvest
and this results in greater sugar yields (1).   In practice, progress-
ively earlier sowing is limited by the possibility of vernalisation of
young seedlings by cold temperatures in Spring, which initiate flower-
ing and bolting later in the season. Bolting reduces recoverable
sugar and interferes with mechanical harvesting. Such agronomic con-
straints on early sowing have been partly overcome by the production of
more bolting-resistant varieties, but the potential for chemical con-
trol is attractive particularly to overcome bolting in the root crop
(4), to eliminate annual weed beet (23) and as a possible means of
realising the potential physiological advantages of Autumn sowing (24).

THE EFFICIENCY OF USE OF INTERCEPTED RADIATION

In a practical sense, the efficiency of use of intercepted radiation must be considered as its conversion to extractable sugar stored in the root. It therefore involves not only the efficiency with which the crop produces assimilate by photosynthesis but the manner in which the plant partitions this assimilate between shoot and root and the way in which the storage root itself partitions assimilate for root growth and sugar storage.

a) Photosynthetic efficiency. The efficiency of the crop in producing the maximum amount of available assimilate per Joule of solar energy intercepted will be governed by several factors. Maximum rates of photosynthesis per unit leaf area and minimum rates of light and dark respiration must be maintained, either directly through adjustments of rates of the biochemical processes involved or more indirectly through prolonging the functional longevity of the leaves. However, under field conditions photosynthetic rate in sugar beet is governed largely by irradiance and factors affecting stomatal aperture. In comparison with other crops sugar beet is relatively inefficient at controlling water loss and experiences considerable diurnal water stresses even under well irrigated conditions (25). Photosynthetic rates will be reduced even under conditions of mild water stress because loss of cell turgor decreases gas exchange through stomata and slows leaf expansion (26,27). Therefore, in the field, we might expect sugar beet to respond more to plant growth regulators designed to improve water status than to those affecting photosynthesis per se or leaf longevity.

It has been suggested that the accumulation of photosynthate in leaves exerts a feed-back control on photosynthesis in circumstances where either translocation is restricted or the capacity of "sinks" is limited (28). There is little evidence that carbohydrate reaches levels that would inhibit photosynthesis in leaves of field-grown sugar beet (29). Moreover, unlike other crops such as cereals and legumes in which the potential size and numbers of grains are limited, the development of the storage root of sugar beet is not restricted and retains a high and continuous potential for growth throughout the season (30).

b)   <u>Partition of assimilate between shoot and root</u>. At present, the
internal mechanism governing the distribution of assimilate in sugar
beet is poorly understood but two aspects are worth mentioning. First,
the manner in which the crop partitions dry matter between shoot and
root is affected by agronomic practices such as planting density and
nitrogen fertiliser.   Both accelerate closure of the leaf canopy and
improve light interception but alter the distribution of dry matter in
favour of shoot growth (12).   In this situation there is a clear opp-
ortunity for a growth regulator which would partition more dry matter
to the storage root so that advantage could be taken from improved
radiation interception.   Second, it has been suggested that the con-
tinued production of leaves in Autumn competes with growth of the
storage root (31).   The inherent pattern of leaf development is such
that these leaves constitute an insignificant proportion of shoot dry
matter and their growth is naturally curtailed by the cold temperatures
and short days of Autumn in Europe (32).   Growth retardants which res-
trict growth of late-season foliage have therefore been less successful
here (31) than in the United States where the crop matures under warmer
conditions (33).

c)   <u>Root growth and sugar storage</u>. In commercial practice both beet
yield and sugar concentration are important.   Sugar yield depends
largely on root yield but factory processing is more efficient with
roots of high sugar concentration.   Root yield and sugar concentration
depend on the manner in which the incoming photosynthate is partitioned
by the root for growth and sugar storage.   Sugar beet establishes and
maintains a constant dry matter sugar percentage early in development,
normally during July, and thereafter sugar accumulation depends on a
continued supply of photosynthate to the growing storage root (2,30,34).
This constant proportioning between sucrose and non-sugar over a wide
range of photosynthate supply is governed by the anatomical character-
istics during development of the storage root.   Several concentric
secondary cambia are initiated early in development and undergo contin-
uous division and differentiation to produce the cells of the storage
root. For instance, the 6-8 cambia which produce over 75% of the root
volume at harvest are initiated early in May when the roots are less
than 10 mm in diameter.   Young, small cells close to the cambia are
relatively more efficient at accumulating sugar per unit volume and
weight than the mature, large cells so that sugar concentration is a
function of the relative proportions of these cells within the root.

It follows that a storage root composed of many small cells would be the most efficient means of accumulating sugar (30). As cambial init- iation and differentiation is probably hormonally controlled, the greatest potential for applied plant growth regulators to increase root size and sugar concentration would be in their use early in the season to stimulate cambial initiation and cell division rather than cell expansion.

The mechanism of sugar accumulation in sugar beet is therefore different from that in sugar cane where growth and sugar storage are competitive. In sugar cane maximum accumulation occurs in tissues that have been laid down previously and is not achieved until plant growth is restricted (35). Sugar accumulation in cane can therefore be enhanced by growth retardants, such as glyphosine (36), which are ineffective in sugar beet (31).

CONCLUSION

We have attempted to define the environmental and internal factors controlling growth of sugar beet at various stages of development and to indicate the processes by which growth and sugar yield might be ben- eficially modified by applied growth regulators. It seems that the control of flowering, the stimulation of early leaf canopy development and the modification of root structure are the most likely means of increasing the sugar yield of beet. This could be achieved either by breeding and selection or by treating present cultivars with growth regulators. An understanding of the role of endogenous growth substan- ces in controlling the various processes should provide a rational approach to the use of regulators. This contrasts with the experimen- tally empirical approach so far used in sugar beet which has not produced responses of sufficient magnitude and certainty to justify commercial exploitation. Nevertheless, we still depend on the chemical industry to produce and screen the necessary growth-regulating chemicals.

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