Concepts for the Application of Crop Physiological Models to Crop Breeding

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Abstract

Many difficulties in the plant breeding process may be attributed to genotype by environment interactions. The present solutions to many of these problems are scientifically empirical and economically costly. Crop physiological models have the potential to be a tool in improving the plant breeding process. The challenge in applying crop models to breeding has been getting the data needed for these models. For simulation models the input parameters generally are very extensive, which means that they cannot be applied to selection among the large numbers of lines handled in a breeding program. However, simpler crop physiological models involving only a few parameters, derived from nondestructive observation, have the potential to greatly improve the efficiency of breeding processes without major changes in data capture and processing capabilities. The techniques advocated can be applied to both improving selection techniques and exploiting the lines generated.

Résumé

Concepts d'application de modèles physiologiques de culture pour la sélection des cultures: *Bien des difficultés dans le processus de sélection végétale peuvent être attribuées aux effets des variations d'environnement et des génotypes qui répondent différemment aux divers environnements. Les solutions actuelles d'un grand nombre de ces problèmes sont scientifiquement empiriques et économiquement coûteuses. Les modèles physiologiques de culture sont potentiellement des outils pour améliorer le processus de sélection végétale. La difficulté pour appliquer les modèles de culture à la sélection a été l'obtention de données nécessaires pour cette modélisation. Pour les modèles de simulation, les paramètres d'intrants sont généralement vastes et cela signifie qu'ils ne peuvent pas être appliqués à la sélection parmi les grands nombres de lignées traitées dans un programme de sélection. Toutefois, des modèles physiologiques de cultures simples, n'impliquant que quelques paramètres et dérivés d'observations non destructives ont un potentiel pour améliorer largement l'efficacité des processus de sélection sans provoquer de grands changements de la saisie des données et du potentiel de traitement. Les techniques recommandées peuvent être appliquées tant à l'amélioration des techniques de sélection qu'à l'exploitation des lignées formées.*

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For logistical reasons breeding for yield is often subjective in the initial phases, and later becomes a largely empirical procedure. This occurs because of the limitations to obtaining better data and details about the processes involved in yield determination in the numbers appropriate to a breeding program. It is by quantifying (and exploiting the known facts about) the yield-determining processes that improvements in breeding efficiency can be obtained.

Models are not new concepts to crop breeders who have exploited other models for many years. A model (Equation 1, attributed to Fisher, 1926) that all breeders are familiar with provides a good basis for discussion of the problems. This model applies equally to single plant and crop level yield variations. Basic to most breeding practices is the acceptance of the phenotype model of yield:

$$Y_T \text{ or } Y_R = G + E + G.E + \delta \qquad (1)$$

which defines total yield (Y_T) or reproductive yield (Y_R) as being due to the sum of the effects of

(G) genetic,
(E) environmental,
($G.E$) genotype by environment interactions, and
(δ) error components.

Crop improvement by genetic manipulation is an expensive and time-consuming process. A major reason for the high cost of the process is the effect of variations of both E and differential genotype response to varying environments ($G.E$) on plant performance. In terms of this model, a low heritability of a characteristic (such as yield) indicates that G is relatively small compared with E and $G.E$. This means that selection for traits such as these is unreliable and inefficient in early generations. The present breeding solution to this problem is to exert low selection pressure on traits such as yield (with the attendant cost increase). The possibility of genotypes responding differently to variations in E requires the breeder to evaluate the material in many environments to permit estimations of the three components of the model (again, a very costly procedure). Even when multilocational trials are conducted, the existence of a large $G.E$ term in the model without information concerning its physiological basis leaves the breeder without a clear idea of how to further exploit the material. However, better knowledge of the physiological basis for the differential responses of genotypes to specific environments offers the potential to maximize yield at the farm level by better exploitation of the appropriate specific varieties (Williams and Saxena 1991).

Technologies that can allow the contributions of E to yield to be better estimated should improve the efficiency with which the breeder can characterize material for its G and $G.E$ interaction, and should greatly increase the speed with which new varieties are produced.

This paper uses groundnut (*Arachis hypogaea*) as a model crop species, but the approach and tools used have an equally important role in other crops [e.g., chickpea (*Cicer arietinum*) – Williams and Saxena 1991; cowpea (*Vigna unguiculata*) – Ntare and Williams (in press); and millet (*Pennisetum glaucum*) – ICRISAT 1991], and crop science disciplines.

Crop Physiological Models Applicable to Breeding

From the breeding point of view, crop physiology has failed to provide technologies appropriate to the large numbers of lines in a segregating population. Crop physiology has often sought to identify single factors that apparently condition a process, and have asked the breeders to set out and combine desirable factors. There are only a few cases where this has been more successful than the breeders empiric selection on the final outcome. The isolation of physiological attributes has probably failed because "yield is a complex terminal outcome of growth to which there are diverse and interrelated developmental tracks" (Simmonds 1979, p. 46).

Just as the breeders have accepted models to help explain the phenomena that they are dealing with, crop physiological models are the expression in mathematical terms of the processes determining crop behavior and yield. Crop models have developed along two main paths. Simulation models are intended to estimate the outcome of a set of conditions exploiting existing knowledge of the factors and processes influencing the subject of the model. Analytical models provide a framework for interpretation of results, based on measurement of the interacting parameters. The most widely promoted application of crop models is for **simulation** (e.g., Boote, these Proceedings pp. 331–343; Shorter et al. 1991). This class of model, usually used to provide estimates of yields given hypothetical (or historical) conditions of weather, has some application to breeding programs and will be discussed later.

However, crop models that provide an **analytical** basis for the determination of yield probably have the most scope for immediate application to improve efficiency in a breeding program. Any model appropriate to breeding programs requires that the parameters of the model be obtainable very simply, without additional investments in manual data collection.

Fortunately, several appropriately simple models have been described by Duncan et al. (1978), (Equation 2); and Monteith (1977) (Equations 3 and 4). In using them, we must recognize that these simple models integrate many complex processes into a single parameter. However, while a full understanding of all the processes is desirable, a great deal more can be achieved by working with these 'integrated' parameters than with yield only.

Duncan wrote simulation models for a number of crops, most of which were an expansion of the basic model:

$$Y_R = C * D_R * p \tag{2}$$

where: Y_R is reproductive yield,
C is the mean crop growth rate,
D_R is the duration of reproductive growth, and
p is the mean fraction of crop growth rate partitioned towards the reproductive organs (Duncan et al. 1978).

In this model C provides a measure of 'source' (an integration of the effects of radiation intercepted by the crop and the photosynthetic result of this). The duration is a relatively simple parameter, while the partitioning parameter provides an integration of the reproductive initiation processes and translocation; p and D_R are terms that describe the 'sink'.

Monteith proposed similarly simple models:

$$Y_R = I * e * H \tag{3}$$

or

$$Y_T = I * e \tag{4}$$

where: I is the cumulative radiation (or light) intercepted,
e is the mean rate of assimilation per unit of radiation intercepted,
H is harvest index, and
YT is total biomass.

Model 4 has been found appropriate for many crops (e.g., Gallagher and Biscoe 1978), including groundnuts (Azam Ali et al. 1989). In most species the major source of variations in Y_T are in I rather than e (which is a conservative parameter).

Duncan's model is probably most easily applied to breeding, and the concept of partitioning is better than that of harvest index, particularly in an indeterminate crop such as groundnut. Monteith's models are significant in dealing in more detail with the determinants of crop growth rate than Duncan's model. However, these models can be combined and manipulated, to produce models to address specific requirements.

As stated earlier, many of the problems that the breeder faces can be attributed to the effects of E and $G.E$ dominating those due to G. Physiological models make the interpretation of this variation a much simpler process, thereby allowing material to be evaluated with greater confidence. Conceptually the components of phenotypic yield can be evaluated within the framework of Duncan's model by distributing these sources of variation between the parameters C, p, *and* D_R. No analyses of this type have been done so far but physiological knowledge of the processes permits the probable relative importance of the yield determining factors in one model to the various components of the other to be hypothesized (Table 1).

Crop physiological knowledge suggests that variations in C are dominated by E and $G.E$ because the photosynthetic variation within a species is small, while the scope for variations in energy interception is very large. The evidence concerning partitioning indicates that genotype differences are very much more important in this area; in contrast environment, with some notable exceptions (photoperiod effects in groundnuts; Flohr et al. 1990), is a less significant source of variation in partitioning. It also seems likely that various environmental challenges will have different 'signatures' in influencing C, p, and D_R. For instance, drought will influence C and p, calcium deficiency will influence p, and foliar diseases will mainly influence C.

Table 1. Hypothetical importance (ranked 1 = minor, 9 = major) of parameters in Fisher's model to variation in the parameters of Duncan's model.

Model parameters	G	E	$G.E$
C	1	9	4
p	7	3	5
D_R	5	5	4

Crop Breeding Procedures and Limitations, and their Physiological Basis

Generally, high yield is an important objective in a breeding program, and it is in the achievement of this objective that models may have the greatest amount to offer the breeder. Although the current methods have achieved varieties with high yield potential, each new hybridization effort requires the breeder to reselect for yield. Additionally, for many crop species breeders realize that there is a yield barrier and I believe that the application of Monteith's crop models to selection provides the best chance of advancing further. The removal of variation due to the environmentally determined variations in energy interception will allow direct selection for efficiency of light use if variation exists within the target species.

A breeding program has several phases. These start with identification and choice of objectives, parental materials, and breeding method. This phase is then followed by production of segregating material, selection, and, finally, evaluation of selected lines relative to existing varieties in environments representative of the target cultivation areas.

Identification of objectives

Simulation models may play an important part in a breeding program in defining the objectives (Shorter et al. 1991). For many proposed changes simulation models should be used for sensitivity analysis to determine if (based on the existing knowledge) the outcome will be as anticipated. This could greatly decrease the uncertainty of success. For example, one could vary the phenology controlling parameters of a variety and evaluate the *probable* impact of these changes on yield using historical weather data. This could guide a proposed change in duration to optimize yield and its stability. However, this approach to objective definition requires very expert knowledge of both the model and the crop.

Choice of parental materials and methodology

Both the breeder and physiologist presently invest considerable effort into this phase of variety development. This effort usually involves study of physiological mechanisms contributing to differences in genotypes, and of the modes of inheritance for traits of interest. This knowledge determines how the segregating material is best handled, and how various selection pressures affect the chances of success. Seed yield commonly has low heritability, and this is reflected in the relatively slow progress to high yield potential in most crop species.

Selection for yield and yield potential

Once the breeder has made his crosses and advanced the product for several generations, his interest centers on reducing the numbers of lines to evaluate in better detail.

How reliable is the seed yield of an individual plant growing in a segregating population, or in relative isolation (test row) as a predictor of future yield? Data of plant-to-plant variability in an apparently uniform crop of breeders seed (Williams 1975) suggests that (even for Y_T) single plants in a population are very poor indicators of the pure stand performance, even without the confounding effects of major genetic differences between plants. In terms of Duncan's model this can be most logically explained by variations in C; Monteith's model indicates that this is likely to arise with variation in energy interception, which is determined largely by environment.

Why is it so difficult to select for yield? What is the physiological basis for this low heritability? At present there are no direct data to answer these questions. We have no published data relating to the inheritance of the individual components of Duncan's model. However, it is probable that the p, and D_R will prove to be more highly heritable than yield, while C will prove to be the factor largely responsible for the low inheritance of yield. Evidence to support this suggestion is only circumstantial. In terms of Monteith's model (4) and by assuming a conservative value for e (based on the extent of variation in e observed within most crop species), the basis for large phenotypic variation in Y_T between plants must be large variation in energy interception by individual plants. This view is supported by the evidence that shows that once light interception by a groundnut crop is complete, the major sources of yield variation between varieties lie in their partitioning and duration (Duncan et al. 1978); the progressive increase in pod yield in the Florida groundnut breeding effort was associated with improvements of partitioning, while C remained constant.

Duration of reproductive growth is another important factor that can make direct selection for yield an imprecise exercise. The potential reproductive growth rate (R) of a good groundnut crop is about 100 kg ha^{-1}

d^{-1}, so comparing yield of crops/varieties with even a small difference in D_R can result in poor decisions about the merits of material.

For groundnuts, Y_R alone also may be confounded because of feedback effects due to variation in p that operate in communities of competing plants. In a population of groundnuts with differing p, low yield potential (based on low partitioning) could result in greater plant yield than from high partitioning plants because high partitioning reduces vegetative growth and therefore limits energy interception (i.e., low partitioning plants are more competitive). In a stand of a uniform genotype, the opposite is the logical outcome of these differences in partitioning.

Therefore, selection on yield alone is likely to be misleading. These problems are most commonly catered for (by the breeder) by employing a low selection pressure, which requires that a larger proportion of the material is retained than would otherwise be necessary. However, if the suggested low inheritance of yield is attributable to variations in C and if the processes determining yield can be quantified at this stage, the breeder could appropriately increase the selection pressure for the more genetically controlled parameters (p and D_R). However, in some cases C needs to be considered along with p and D_R because factors, such as foliar disease resistances, will impact mostly on C.

Advanced evaluation

As the breeder reduces the number of genotypes he usually increases the objectivity of his evaluation. He has enough uniform material to test in replicated trials and then to expand these to varied environments. In the final stage of the breeding process the breeder compares the material that has survived his selection process across sites and years to select the most adapted genotypes. At this stage one has to face the possibility that the agronomic practices necessary to maximize the yield of a specific variety may be different from those used as a standard in the evaluation.

Evaluation of trial results using the physiological model determinants of yield rather that yield itself can make clearer the reasons for yield differences, and so guide the further exploitation of material and provide insights that can result in modified screening techniques, and thereby provide more efficient breeding programs. For example, a variety that is failing to yield well in pure stand because of low C is likely to be doing this because of relatively low light interception, and, if it has enough other attributes to recommend it, would justify agronomic manipulation, e.g., higher populations.

Practical Application of Models

To apply these models in a program it is necessary to obtain data for the parameters of the model at the level of the single plant or plot. How can this be done? Traditionally, physiologists have measured the parameters of these crop growth models using destructive growth analysis, a requirement that has prohibited the widespread use of these techniques. However, recent research at ICRISAT has shown that this costly data collection is not necessary for comparative purposes. Only measurements of defoliation percentage, total and pod (or seed) yield at maturity, and phenological observation to fix the start of grain growth and maturity are needed to provide relatively good estimates of C, p, *and* D_R. Observations of radiation interception can refine this data further, but are not essential for many breeding applications. Data for the yield determining parameters can be obtained by two techniques. Firstly, by 'reverse engineering' these simple models one can estimate the parameter C and R that would have resulted in the observed final Y_T and Y_R, (Williams and Saxena 1991). This is most easily done using a linear estimation of growth. However other models, for instance Goudriaan and Monteith's (1990) expolinear model (which would need more advanced "math solver" programs), may provide more accurate estimates of C and R.

Secondly, remotely sensed data for fractional light interception [which may be obtained for groundnuts very cheaply using the differences in reflectance of red and infrared radiation (see Figure 1)] can be combined with incident radiation to estimate the Y_T or C from Monteith's models. Current research at Washington State University, USA, and ICRISAT's Sahelian Center (ISC) is evaluating this second approach. The radiation data can be used to better distribute the accumulated dry matter across time and so improve the estimation of p since Y_T over the reproductive phase can be better estimated.

Partitioning has been traditionally estimated as $R \div C$ (Duncan et al. 1978). A comparison of p obtained by 'reverse engineering' with that obtained by conventional growth analysis during the season is presented in Figure 2. The data are from an experiment where photoperiod effects on growth of genotypes were evaluated.

The data on final yield, total biomass, and days to flowering and maturity needed to estimate the para-

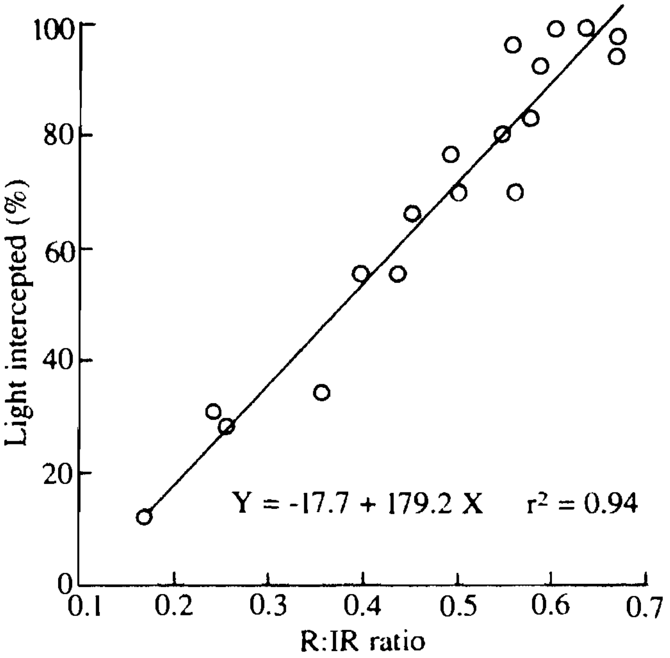

Figure 1. Light interception related to normalized red:infra-red reflectance ratio for groundnuts. (Source: Rao et al. 1992.)

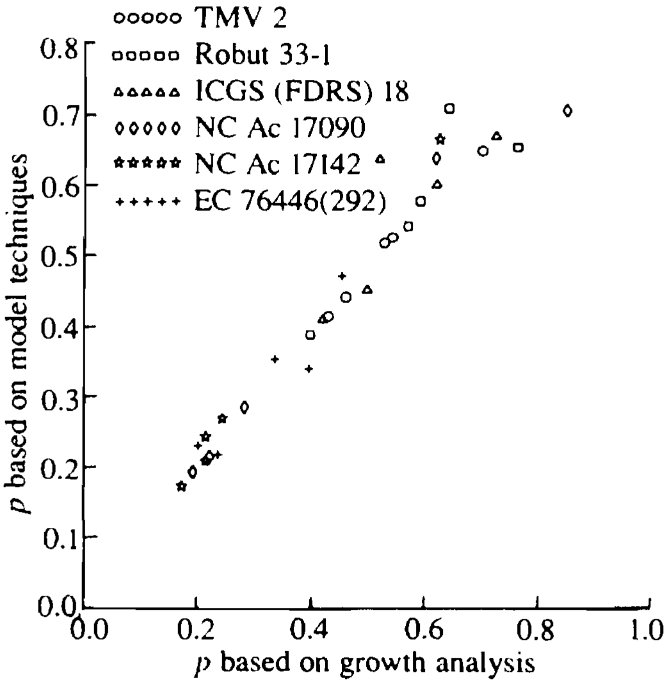

Figure 2. The relationship between partitioning (*p*) estimated directly from growth analysis and partitioning estimated from nondestructive (peripheral) observations. (Source: Unpublished data of Williams, Ramraj, and Devi.)

meters of Duncan's model are mostly already collected by breeders. Only modest computers are needed to do the calculations.

So far no breeding programs have results based on applying these 'model' approaches to selection within segregating populations. However, Greenberg et al. (1990) have shown that all the lines adapted to the Sahelian environment maintained superior *p* when grown in the very hot summer at ISC with full irrigation. The ISC program is now using nondestructive observations in small plots and these 'model' techniques to estimate partitioning of large numbers of lines. This past season some 625 lines were evaluated in this way.

An Example

Since no results are yet available from selection based on this approach, the best example available is provided by the application of these ideas to the interpretation of data relating to varietal adaptation to Sahelian conditions. The analysis used as an example resulted in the application of these techniques to selection for *p* at ISC.

The model approach was applied to the data collected in a series of trials comparing genotypes adapted to the Sahelian environment with those from other origins. In the experiments 35 groundnut genotypes were grown in 5 environments where the water (as a fraction of pan evaporation) and temperatures were manipulated by sowing dates and irrigation (Greenberg et al. 1990).

The necessary phenology and final yield data, and the midday canopy temperatures were collected in the summer experiments. After the durations of phases had been converted to thermal time and the weights adjusted for the higher energy values of pods, the parameters of Duncan's model for all 175 treatment combinations were computed. The growth rates (*GR*) for both *C* and *R* were computed as the linear growth rate between sowing and maturity with the standard equation:

$$GR = (Y_2 - Y_1)/(T_2 - T_1).$$

A standard stability analysis (Finley and Wilkinson 1963) was then applied to the determinants of yield (*C* and *p*) rather than the yield data. The mean *C* in each environment ranked according to the fraction of potential evapotranspiration that was satisfied, a result to be expected considering the role of water relations in canopy and leaf area development. However, what was surprising was that the adapted Sahelian varieties were only average for their *C* in the water deficit environments. Genotypes from other environments had greater C in the water deficit environments (Figure 3a).

Canopy temperature (based on air temperature and air:canopy temperature relationships) varied considerably in the environments, being lowest in the rainy season, intermediate in the hot season with full irrigation and increasing further as the water supply decreased in the hot season. The mean partitioning of the environments increased with lower canopy temperatures. In the normal rainy season all the genotypes had high partitioning, and this declined as the environments became drier and hotter (Figure 3b). However, the Sahelian-adapted genotypes maintained their partitioning at higher levels than nonadapted genotypes in the hotter environments, particularly so in the fully watered summer environment. Thus, tolerance of p to high temperature is apparently more important to groundnut adaptation in the Sahel than superior crop growth rates in the face of limited water.

Conclusion

There is clearly a case to exploit the use of crop physiological models in a breeding program. Simple analytic models may be exploited without major additions to the data gathering exercise that most scientists undertake, and should materially increase the value of the data gathered. The improved information thus available can or may improve the speed of research progress and result in greater satisfaction to the scientists involved.

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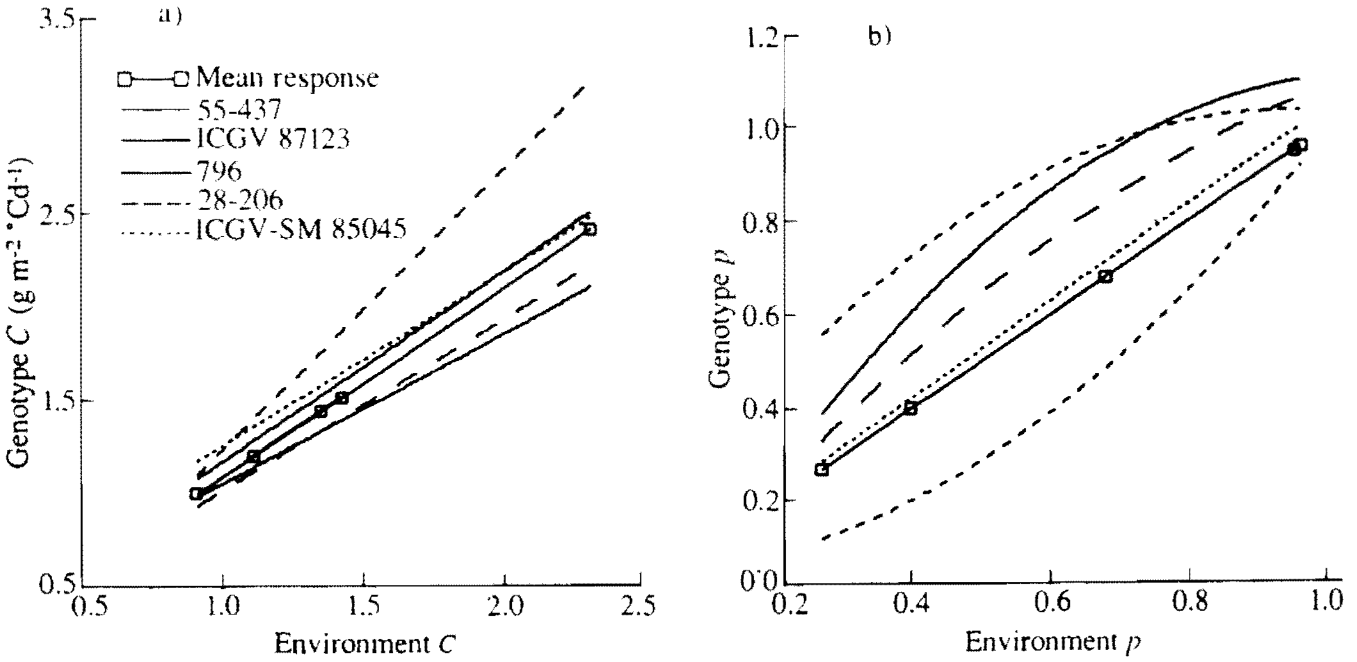

Figure 3. Stability of mean crop growth rate (*C*) and partitioning (*p*) for genotypes adapted and nonadapted to Sahelian conditions exposed to environments with varied water supply and temperature conditions.

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