The implications and applications of resource capture concepts to crop improvement by plant breeding

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Abstract

Models relating crop production to resource capture and resource use efficiency (RESCAP) may be combined with the phenotype model applied in breeding that identifies sources of variation for traits. Estimating the parameters of the RESCAP models with low-cost non-destructive methods can improve the attribution of sources of variation in the phenotype model and, therefore, improve breeding efficiency. Since the resource captured is largely environmental(E), determining the contributions to yield from this source can leave a better estimate of the genetic(G) and $G \times E$ contributions to the phenotype. Some of the potential or existing applications include:

(a) breeding for productivity through improved resource capture and/or use efficiency, and screening materials for difficult traits such as root traits in drought resistance/tolerance breeding programs;

(b) evaluation of crop improvement strategies. Decisions about selection priorities and sequences depend on the relative extent of genetic and environmental contributions to variation. The RESCAP approach allows the relative components of the phenotype model to be estimated cheaply and aids in their interpretation;

(c) improving statistical analysis of breeding trials by exploiting the non-destructive growth analysis of plot yields to isolate the genetic contributions to yield within trials with large error terms due to non-systematic environmental effects and

(d) improved selection for yield in early generation segregating populations. RESCAP based on non-destructive single plant and small plot (row) growth analysis and the different contributions of RESCAP model parameters to the phenotype model terms effectively increase the heritability of yield with the attendant possible changes in plant breeding efficiency and practice. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Resource capture (RESCAP) models have been successful in describing in simple terms the productivity of crops and plants in varied environments. The goal of this paper is to show how they relate to crop breeding, and how they can be applied to improve the processes of crop breeding and crop improvement. RESCAP and the various models applied in breeding are only dealt with in sufficient detail to explain the links between the respective crop improvement endeavors. Many of the references used to justify the arguments are drawn from the peanut literature, but comparable references do exist for other crops.

Physiology is an integral aspect of all crop science disciplines since (by definition) it is the study of processes. Breeding for yield improvement always has manipulated the processes by which yield has been achieved, but most commonly the selection has been guided by empiric results for two important practical

reasons. Firstly, quantifying processes has usually been too time consuming and costly for this to be applicable to the numbers involved in segregating populations and breeding programs. Secondly, very often single processes do not dominate the determination of yield, so selection for a single process is inappropriate. However, many of the avenues of crop improvement that were easily exploited by the empirical approach have now been traveled and the rate of progress has slowed. If productivity is to be increased into the future then increasingly more complicated and subtle differences have to be detected and exploited for crop production in their specific environments. RESCAP models provide a practical solution to some of these problems and although there are few case histories to draw on, this paper aims at demonstrating the approach and the numerous potential applications of the approach to crop improvement and breeding for higher yields.

The basis of the resource capture approach is that productivity of any process is the product of the amount of resources captured and the efficiency with which these are used in producing the desired product (Eq. (1))

$$Y = P\epsilon \tag{1}$$

where Y is the product, P the resource used, and ϵ is the resource use efficiency term.

The approach is usually valid for both systems and subsystems of our environment. The really important benefits of the resource capture model applied to crop improvement stem from the fact that the model expresses productivity as the outcome of three integrative parameters relating to the acquisition of resources, their conversion to biomass and the distribution of this biomass into the economically important part of the crop. The amount of resource captured is determined by the availability of that resource and the management that the crop experiences, both being predominantly environmental determinants of crop production.

Malthus' prediction that population would expand until resources became the limiting factor has so far been postponed despite the dramatic growth of the world's population. This achievement has occurred because of the exploitation of new resources or because of increased resource use efficiency. From the practical viewpoint, increased food production has been achieved by opening up new areas of production,

increasing the water resource of these areas through irrigation (increasing the extent of resource capture — P) and increased productivity of existing areas (resource use efficiency term — ϵ). However, as with most resources there are finite limits to resources and over much of the world the costs (both environmental and economic) of expanding production areas suggests that we are approaching the limits to increasing productivity through increased resource exploitation. Greater production must increasingly be achieved by improved resource use efficiency, and crop manipulation through genetic selection (breeding) and environmental manipulation (agronomy) have been (and remain) important tools in the achievement of the needed increase. RESCAP approaches are relevant to both genetic and environmental manipulation of crop production, and to the decision about which one is likely to be the most appropriate to manipulate. Effective crop improvement programs should always address the range of constraints to productivity through the most effective approaches. As will be discussed at greater length later, knowledge of where the gains are most likely is also important in maximizing the efficiency of improvement efforts.

The process of crop breeding is determined by the genetics of the crop and the environment, and the majority of practices used are driven by the cost of examining plants for different attributes needed in the final product. Costs of evaluating traits usually decides the order in which they are evaluated. Attributes that are highly heritable and easily quantified are used to narrow the field before further (more expensive) tests are used, often despite the fact that these attributes may be of lesser importance to the success of a variety. Yield and quality are often evaluated last, despite the fact that they are usually the most important, because of the high cost of quantifying these attributes and the relatively large amounts of seed needed for these tests. Many breeding practices are aimed at identifying crop/plant responses/attributes against a background of variable expression of genes. Breeders are always searching for the most uniform soils (environments), marker genes or correlations between attributes that can ease the screening process.

Because of the large number of possible combinations in a segregating hybrid population, process-based aspects of performance usually are only considered as contributions to breeding as traits of parents. These

attributes are introduced into breeding programs at this stage, but are seldom subsequently selected for directly because of the cost and numbers involved. However, with the RESCAP approach there is scope for process level evaluation of segregating populations for attributes such as yield, rooting differences and water use efficiency to be selected for in segregating populations, with the attendant changes in the overall practice of breeding.

2. The generic resource capture model

The generic resource capture model which can be adapted to describe the relation between production and resource use for any particular resource is expressed in Eq. (1). In the crop context, this model is most commonly applied to light and water, but is also valid for nutrients. An alternate version of this model (Eq. (2)) expresses the crop growth rate (C) as a function of the rate of resource capture ($\delta P/\delta t$), the resource use efficiency term.

$$C = \frac{\delta P}{\delta t}\epsilon \qquad (2)$$

This version is more dynamic and make the RESCAP models sensitive to temporal variations in resource availability.

Where a component of the crop is harvested as the economic product this is catered for by adding the harvest index term (h) to Eq. (1) and a partitioning factor (p) applicable for the duration of the reproductive phase (D_R) to Eq. (2). This links the RESCAP model with the model (Eq. (3)) used by Duncan et al. (1978) to analyze the physiological basis of crop improvement for peanuts (*Arachis hypogaea* L.).

$$Y = CD_R p \qquad (3)$$

Following the application of the RESCAP concepts to analysis of crop production (Monteith, 1977) there has been considerable effort in validating them for various crops and production circumstances. The original concepts (linear relationships with conservative resource use efficiency) have been validated for many crops in regard to water (Matthews et al., 1988) and light (Azam-Ali et al., 1989) as summarized by Monteith (1990). The major thrust is now on the application of this model to practical problems.

There have been a number of different ways in which the model has been applied. Provided that resource capture can be predicted or described, primary productivity can be simulated (Goudriaan and Monteith, 1990), and if the harvest index is known, economic yield can be predicted (e.g. Azam Ali et al., 1993; Campbell and Stockle, 1993). A further application is non-destructive growth analysis based on cumulative light interception throughout the crops life and light use efficiency (e) estimated from measured final biomass (Williams et al., 1996).

Since radiation is one of the major driving forces for water use, it follows that there is usually a similar relationship for the light and water models, and depending on convenience one could choose to use either with equal reliability in many circumstances. However, the influence of water supply on stomatal resistance means that when water is the limiting factor the e term of the radiation model is not maintained (Azam-Ali et al., 1989; Campbell and Stockle, 1993). However, in some crops, short term changes in leaf orientation (e.g. Matthews et al., 1988) and the long term adjustments to leaf area (Monteith, 1977) operate to keep these changes relatively small. Despite the mechanisms which operate to keep energy interception (I) in phase with water supply, it is necessary to vary the radiation use efficiency term or to select the RESCAP model based on the most limiting aspect of the environment (Campbell and Stockle, 1993) for successful crop growth simulation purposes.

Since the resources involved in crop production and their capture are subject to manipulation by the farmer, it is necessary to briefly mention the relevance of RESCAP to agronomy. Much of agronomy is the manipulation of resource capture to maximize productivity of the economic fraction of the crop. For example, the optimum sowing dates and plant spacing of most crops provide for optimizations of resource capture (either light or water) within the limits of the season and crop phenology; fertilizer recommendations optimize leaf area and increase light capture.

2.1. Quantifying the RESCAP model's parameters

Traditionally RESCAP models have been validated by regular observation of the amount of resource captured over intervals of time and associated growth measurement of biomass, leaf area and growth

distribution by destructive sampling. These growth measurements are too labor intensive for application to plant breeding. However, D_R is usually available in datasets since flowering and maturity dates are commonly observed; and valid mean values of C and p can be estimated from the data usually commonly collected in breeding programs (flowering time, maturity time, total biomass, and reproductive yield) (Williams, 1992). More precise measurement of C through time is possible from the measurement of fractional light interception at intervals during crop growth by direct measurement, or the use of image analysis techniques and reflectance methods (Gallo et al., 1993). These observations coupled with the final biomass allows mean radiation use efficiency to be measured (Williams et al., 1996). Water use efficiency can now be measured using carbon isotope (ΔC) methods (Hubick et al., 1986; Condon et al., 1990), and more recent research (Nageswara Rao and Wright, 1994) shows that specific leaf area (SLA) is well correlated with water use efficiency (w) in peanut.

3. The phenotype model

Breeders across the world have implicitly and explicitly exploited a model (Eq. (3)) which separates variation in observed plant/crop attributes (A) into those associated with genotype (G), environment (E) and the genotype by environment interaction ($G \times E$).

$$A = G + E + G \times E \qquad (4)$$

Within the $G \times E$ we are able to consider two components, according to their origin, which are relevant to the application of plant breeding. RESCAP based $G \times E$ ($G \times E_R$) describes differential performance of genotypes due to differences (such as canopy attributes) that can be easily manipulated by agronomy (plant spacing etc). In breeding programs, this $G \times E_R$ is a potential source of error since it confounds performance in segregating populations and provides bias towards types having attributes which cease to be important when in a pure stand of that genotype after agronomic optimization.

The phenotype model (Eq. (4)) is fundamental to crop breeding. Most of the breeding strategies, tactics and practices can be explained in terms of the phenotype model. For instance, the timing and order of selection for various traits is dictated by the relative contributions of the three components of the model to the expression of the traits. When G is the predominant source of variation selection is usually reliable and practiced in the early stages of the breeding process, when variation in E is the dominant source the reverse applies. The heritability of traits is related to the relative sizes of the G and E variation. The testing of lines in multi-location trials is mandated by variation in E and $G \times E$. The wide or narrow adaptation of genotypes is reflected by the relative sizes of the parameters of the model.

An important aspect of the phenotype model is that it is equally applicable to all levels of the consideration (individual plants within crops, to plots within experiments, and to experiments across sites and years), but the source of environmental variation changes in each situation. Breeding programs tend to focus on environments as the gross differences between locations and years at these locations. However, the other levels of the environment are equally important to the practices of breeding. Within an experiment the role of experimental designs is to define systematic E effects, while the error term of statistical analysis contains those contributions to variation from other environmental sources. The plant breeders' need for uniformity within experiments, and the ability to determine differences is determined by the magnitude of unquantified environmental variation. The environment of single plants within plots or rows includes the competitive effects of neighboring plants, which if genetically different (as in segregating populations) may generate $G \times E$ effects which confuse selection. For example, a plant with genetics for low partitioning to fruit and vigorous vegetative growth may have higher yield than a plant with the opposite attributes when in a mixed stand, but in pure stand the relative performance would change. The practice of selecting among spaced plants reflects the need to minimize competitive effects. Breeders at present avoid dealing with these effects rather than quantifying and exploiting them, but the RESCAP models could change that.

The RESCAP models are relevant at all levels of the breeding environment since RESCAP principles are relevant to the performance of individual plants in segregating populations, to single rows of plants, to plots being compared within advanced generation trials, and to genotype performance in multi-location

trials. Since RESCAP models deal with the environment they are potential tools to assist in the separation of environmental effects from genetic effects.

3.1. Quantifying the phenotype mode/parameters

The phenotype model is implicit in a very wide array of agricultural experimentation. Statistical methods dominate the separation of variation into the components of the model, and two main applications which quantify the contributions of the terms of the phenotype model to yield can be identified. The first and obvious application is the statistical analysis of variety trials conducted in multiple environments. In the wide sense of the phenotype model, any trial which examines the response of varieties to a range of agronomic treatments is deriving the terms of the model. Another example is provided by the common experimental designs and analysis of variance of variety trials with replications. In this case, the block structures of the various designs are attempts to quantify systematic environmental contributions to the overall variation; and the error term of these analyzes is the unquantified E and $G \times E$ effects.

The second application of the phenotype model is the estimation of heritability by various methods. When heritability is high the genetic contribution to overall variation is large, when heritability is low, overall the variation is implicitly attributed largely to environment. Because of the difficulties in quantifying the environment of a single plant, no attempts are made to separate out the phenotype model terms operating at this level. Breeders will often examine spaced plants, but this is usually for highly heritable attributes (not yield) because of the differences between the test environment and the normal production environment.

4. Inter-model links — the RESCAP models in terms of the phenotype model

The parameters of the RESCAP model can be analyzed in terms of the parameters of the phenotype model, at any scale of environment. Thus the contributions of G, E and $G \times E$ to P or $(\delta P/\delta t)$, ϵ, and (h or p-distribution of primary productivity into the economic component) can be determined. However, there is little direct study of these relationships, and much

must be inferred from other studies. This will be done by reviewing the available evidence for E, G and $G \times E$ effects on variations in P or $(\delta P/\delta t)$, ϵ, and h or p.

4.1. Resource capture

The possibility of very large environment or management determined variations in the P or $(\delta P/\delta t)$ across sites cannot be disputed. Variations in P may be plant/crop or environmentally determined by either the resource capture apparatus, or the flux/reservoir of resource. However, the nature of resource based variation changes with the scale of environment. The amount of rainfall, radiation, cloud, disease pressure and humidity are usually comparable within a site and differ mostly between sites. Within an experiment or field, factors such as soil water storage potential, and nutrients can be responsible for major differences in canopy or root development, and, therefore, determine resource capture. Within a plot of foundation seed of peanut (which has a very low out crossing rate and for which the G component may be considered small) the evidence of large individual plant shoot weight variation (Williams, 1975), suggests that P varies substantially at the individual plant level due to competition for light. This variation is likely to be a major contributor to the generally low heritability of yield since plant yield varied substantially despite very limited genetic variation.

Also important to the application of RESCAP models to breeding is the possible extent of G or $G \times E$ contributions to variation in P. These have to depend on genotypic variation in the resource capture apparati (root systems, or canopies). Such variation clearly exists, for example, the leaf area that individual plants of genotypes generate may vary substantially, but these differences can be compensated for by adjustments of population and/or plant arrangement, and are, therefore, (by definition) $G \times E$ interactions that can be manipulated by agronomic practice. It follows that much of the variation in primary productivity between plants may be attributed to the E term of the phenotype model or to $G \times E_R$ that is subject to manipulation by agronomic practice. This conclusion is consistent with that of Monteith (1977). Whether that agronomic manipulation of P or $(\delta P/\delta t)$ is desirable or feasible is not important to the application of the model to separating out the terms of the phenotype model.

4.2. Resource use efficiency

The evidence for variation in ϵ attributable to E is substantial, but generally the extent of the variation is relatively small (Monteith, 1977).

The extent of variation in ϵ from genetic sources is also relatively small, but potentially significant. Numerous studies have examined the germplasm for variations in photosynthetic response to light, or light use efficiency in many crops (reviewed by Tanner and Sinclair, 1983). In peanut, although there is substantial genotypic variation in photosynthetic rate for single leaves (Pallas and Samish, 1974; Bhagsari and Brown, 1976) these differences are not easily detected in the field where differences in canopy structure and leaf orientation apparently operate to minimize differences (Williams and Boote, 1995). Further, Sinclair (1993) argues that the majority of the variation reported is associated with physiologically 'crippled' lines and reflect lower than normal photosynthesis rather than rates above the average of genotypes that are relevant to breeding. Once energy interception is complete, variations in C between genotypes is usually very small (Duncan et al., 1978; ICRISAT, 1983) for well managed crops. The major differences in w between species exploiting C_4 and C_3 pathways is well documented (summarized by Tanner and Sinclair, 1983). The variation within a species is much less pronounced, but none-the-less potentially important for crop improvement. The evidence for variations in w within a species has attracted considerable attention over the past decade following the demonstration by Farquhar and Richards (1984) that differences existed between genotypes of many C_4 species and that these could be measured with relative ease using carbon isotope discrimination (Farquhar et al., 1986). Approximately two-fold variations in w have been reported for peanuts (Wright et al., 1994), wheat (Condon et al., 1990), and beans (Ehleringer, 1990).

Genotype×environment interactions for light use efficiency (e) are also real possibilities. Potentially, genotypes with greater rooting which provides for more open stomata during a drought would have a higher e than those that lacked this attribute. Genetic differences in tolerance to nutritional disorders such as iron deficiency, would also create variations in e. Similarly, genetic differences in foliar disease resistance would generate differences in e since healthy

tissue would continue to photosynthesize at a rate different to that of diseased tissue while both would be intercepting light regardless of the disease situation. However, data quantifying the extent of $G×E$ for ϵ from nutrients and diseases are yet to be published.

4.3. Growth distribution

Variations in p or h associated with environment are large and well documented. In many cases the presence of reproductive structures is determined by the success of pollination, and this is subject to temperature, water and nutrient status, the presence or absences of pollinators and many other environmental factors. Many environmental effects on p are also attributable to variations in the resource during the time that the economic component of the crop is being generated. This occurs because it is usual that current photosynthesis is the dominant source of dry matter for seed (the usual economic plant structure).

However, the variation in p attributable to G may also be substantial. Duncan et al., 1978 found that the consequence of sustained selection for higher yield within the Florida peanut breeding program had to increased p, without significant improvements in C. Similarly there is also good evidence from maize, sorghum, wheat and rice and many other crops to show that genotypic differences in p or h are important to the determination of grain yield within a given environment at plot or site levels. The scope for $G×E$ interactions to occur for either partitioning or harvest index is also significant (Williams and Saxena, 1991), usually being dependent on phenology providing for differential escape from resource limitation.

In summary, the evidence from many trials and studies indicates that the major part of variations in crop growth rate can be associated with variation in resource capture, that partitioning is largely determined by G and $G×E$.

5. Actual or possible applications to crop improvement

5.1. Breeding for productivity through increased resource capture or resource use efficiency

Although the majority of variation in P have been attributed earlier to E and manageable $G×E$ there is

still a significant effort focused on the exploitation of RESCAP in breeding programs focused on drought resistance or tolerance. This effort has been encouraged by the finding of significant genetic variation in *w* in a range of crops as detailed earlier. However, an obvious advantage of RESCAP to the improvement of crop productivity in drought situations is that it reduces to a manageable number of integrative attributes the many drought resistance traits and mechanisms. RESCAP deals with attributes such as osmotic adjustment (Ludlow, 1987), root depth (Ketring, 1984), root penetration rate (Kalfaoui and Havard, 1993) or distribution (Nageswara Rao et al., 1993) in a single measurement. Many of these attributes are too difficult, or costly, to measure at any stage of a breeding program other than to influence parental selection. But when considered as contributing to the parameters of the RESCAP model, we have the potential to identify the best existing combination of such individual traits from within the segregating population because the parameters of the model can be quantified with relative ease. Although the transpiration (*T*) term of the model is difficult to determine by direct measurement, it is possible to obtain comparative estimates of *T* by the measurement of biomass at maturity and *w* using Δ carbon — (Farquhar and Richards, 1984); or for peanuts, specific leaf area (SLA) — (Nageswara Rao and Wright, 1994).

Direct selection for *w* in breeding programs has been advocated and is being attempted in a number of programs (Johnson et al., 1990; Ismael and Hall, 1992; Nageswara Rao and Wright, 1994). However, the outcome is at present not clear. Simulation of responses to varied SLA and water-supply levels (Williams and Boote, 1995) has shown that the observed negative correlations between *w* and *p* (Wright et al., 1988) and between SLA and *w* (Nageswara Rao and Wright, 1994) optimize pod yield of peanuts at low *w* for most realistic production conditions.

5.2. Improvement opportunity analyzes

Agricultural research is expensive and much of the justification for modeling lies in the potential of this approach to determine the likely outcome of a management or breeding change. This is particularly important for breeding programs where the time from start to end of a process is measured in years; vari-

eties are usually released some 8–12 years after the hybridization has been made. Given this time horizon the cost of a wrong decision can be substantial, both in resources and lost opportunity. Study of the present level of resource capture, resource-use efficiency and partitioning will determine whether the solution is best achieved by breeding, or other management options. If the available resources are not being fully exploited, then management is probably the best route to yield improvement. An example of this is provided by the rate of nitrogen fixation in peanuts.

There is good evidence (Nambiar et al., 1982) that genotypes may have substantially different nitrogen reduction capabilities (as measured by acetylene reduction). On the strength of this variation, ICRISAT initiated a N-fixation crossing and selection program to try and improve N-fixation (ICRISAT, 1981). However, a subsequent RESCAP analysis (Williams et al., 1990) of this variation found that the majority of the variation was associated with light interception, and was, therefore, management sensitive $G \times E$ so breeding was not the best crop improvement strategy. Variation between germplasm lines in N-fixation per unit light intercepted was very small.

5.3. Improving statistical analyzes of breeding trials

The opportunity to improve statistical analysis of breeding trials exists where variation within the trial site is large, and is not isolated by the experimental design. Doing this depends on the assumption of a dominant contribution of *P* to the *E* term of the phenotype model, and a relatively small *G* variation for ϵ. If one accepts these assumptions about the relative values of parameters, it follows that majority of variations in *C* are attributable to local environmental effects. Then the estimation of *C* from the total biomass and the growth duration generates a covariable which contains a large proportion of *E* which is otherwise accumulated into the error term in the analysis of variance. A screening trial at ICRISAT's Sahelian Center in Niger is used to demonstrate this opportunity. This site typically has coefficients of variation between 25 and 35% (ICRISAT, 1987). In this example, 256 germplasm lines were being evaluated for performance in the summer season when temperatures are high. A balanced lattice design was used, but there were no significant genotype effects

in the conventional ANOVA table for yield. However, estimation of C and the inclusion of C as a covariate in the analysis resulted in the germplasm variation being significant ($P>0.01$). Retesting of lines selected from different sections of the rank distribution after the covariate analysis showed a good correlation between performance across years (Ntare and Williams, unpublished).

A further application of this approach exists in the analysis of multi-location and multi-year cultivar trial series. The estimation of the terms of Eq. (3) and their evaluation using the stability analysis methods (Finley and Wilkinson, 1963) allows the interpretation of the basis for stability, and provides scope to identify how differential cultivar management may be exploited to widen the geographic adaptation of varieties (Ntare et al., 1993; Adomou et al., 1997). An alternate method of detecting these opportunities is the inclusion of C as a covariate in multi-site/year analyzes. The extent that C (as a covariate) reduces the $G \times E$ interaction in such an analysis should be an indication of the scope to adjust management at sites to maximize the performance of varieties. However, analyzes of the latter type have not been published to allow the method to be evaluated.

5.4. Selection for yield in segregating populations

The opportunity to apply the RESCAP model to selection for yield also depends on the assumptions described in the application of RESCAP to experimental analysis. The potential impact of this approach to breeding practice is substantial since in principal making these assumptions allows one to separate the E and management sensitive component of the $G \times E$ from the phenotypic variation, effectively increasing the heritability of yield. Alternatively, this suggests that direct selection for D_R and p will be more effective than selection for yield. With higher heritability of yield many breeding programs could consider selecting for this attribute in larger populations, or at earlier stages of the breeding process. In theory this change should result in more efficient breeding programs. Two potential methods of exploiting RESCAP to do this seem possible. Firstly, one could use the non-destructive method (Williams and Saxena, 1991) to estimate the expanded (E and $G \times E_R$; G and $G \times E_O$) terms of Eq. (3) for individual plants in a segregating

population growing in normal crop conditions. Using C as a covariate would adjust for the majority of differences in P created by the competitive differences of between genotypes and for other local effects (such as small variations in plant spacing and sowing depth) that may provide individual plants an advantage. The other approach would be to use spaced plants and either use the method described above, or to quantify resource capture of these individual plants using serial estimations of light interception (I) by image analysis, or reflectance, techniques. This latter approach would provide an estimation of e which is probably the major source of genetic contributions to variation in C, and potentially allow genetic selection for increased primary productivity.

The justification of, or support for, these assumptions is important. Measurement of the heritability of the determinants of yield in Eq. (3) have not been widely researched. However, data from peanuts in progeny rows (Ntare and Willams, 1997) show that the broad-sense heritability of p is higher ($h^2 = 0.17$–0.79) than that of pod yield ($h^2 = 0.0$–0.45) or C ($h^2 = 0.09$–0.35).

6. Conclusion

The application of RESCAP models in breeding has to be guided by common sense. The evidence of model validations, the limited experience where RESCAP has been utilized in breeding programs, and the known extent of genotype variations in the parameters of these models suggest that there is good scope for these models to improve breeding programs. The potential importance of RESCAP to heritability and to breeding practice in selection for yield is large, but have not yet been widely applied in breeding programs. The models may improve selection for yield, statistical precision of genotype experiments, and provide better understanding of the determination of yield within plots, between plots and between sites.

7. Nomenclature

C	crop growth rate
D_R	duration of reproductive growth
E	environmental variation

G	genotypic variation
$G{\times}E$	variation from genotype by environment interactions
$G{\times}E_O$	variation from genotype by environment interactions associated with other sources
$G{\times}E_R$	variation from genotype by environment interactions associated with resources captured
I	intercepted light
P	resource captured
SLA	specific leaf area
T	transpiration
Y	product
e	light use efficiency
h	harvest index
p	partition factor
t	time
w	water use efficiency
ϵ	resource use efficiency

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