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LIMITATIONS TO THE USE OF PHYSIOLOGICAL VARIABILITY IN PLANT BREEDING[1]

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The possibility that breeding programs may be reaching a point of limited progress because of the lack of genetic diversity has often been raised. However, there is also an often-expressed feeling that considerable genetic variability may exist in fundamental physiological processes. In this review, an attempt is made to examine whether there is evidence of genetic variability in quantitative physiological characters, and if so, whether such variability is likely to be useful to crop improvement programs. The results, presented from the literature and the author's laboratory, indicate that physiological characters demonstrate considerable genotypic variability in expression. Moreover, in cases where genotype performance has been studied over a range of environments or where crossing studies have been carried out, physiological characters often have relatively high heritabilities. This suggests that, at least from a genetic standpoint, improvements in the expression of physiological processes may be possible. On the other hand, the problems of environmental sensitivity and its resultant error variability, combined with cumbersome methodology and complex physiological interactions, make it difficult to relate individual physiological characters to agronomic benefits, and make large genetic studies difficult. The exploitation of physiological diversity remains a major challenge to plant scientists.

Key words: Genetic heritability, physiology of yield

[Limite à l'utilisation de la variabilité physiologique dans l'élevage des plantes]
Titre abrégé: Physiologie et élevage

On fait souvent allusion à la possibilité que les programmes de sélection génétique soient en voie d'être plafonnés pour le manque de diversité génétique. Cependant, on entend aussi souvent dire qu'il existe une variabilité génétique appréciable dans les processus physiologiques fondamentaux. Dans cet article analytique, l'auteur traite de l'existence de la variabilité génétique des caractères physiologiques quantitatifs et de l'utilité de celle-ci dans les programmes d'amélioration des cultures. Selon la bibliograhie et les résultats d'expériences réalisées par l'auteur et ses collaborateurs, il semble que l'expression des caractères physiologiques montre une variabilité génotypique considérable. Il apparaît de plus, à la suite d'études sur le comportement génotypique menées dans une variété de milieux ou dans le cadre d'expériences de croisement que les caractères physiologiques ont souvent un degré d'héritabilité relativement élevé. Cela porte à croire que du point de vue génétique tout au moins, l'amélioration de l'expression des processus physiologiques peut être possible. D'un autre côté, les problèmes de sensibilité aux conditions du milieu et la

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variabilité erratique qui en découle, ainsi que les méthodes d'analyse peu pratiques et les interactions physiologiques complexes, rendent difficile de cerner les relations qui existent entre un caractère pshysiologique particulier et ses avantages agronomiques, et représentent une entrave à la réalisation d'études génétiques de grande envergure. L'expploitation de la diversité physiologique présente un défi de taille pour les botanistes.

Mots clés: Héritabilité génétique, physiologie du rendement

The productivity of a crop can be limited by any of the physical properties of its environment. However, the concept of environmental limitation is meaningful only in reference to a specific plant type, since the productivity of crop species or cultivars can vary within a single environment. The physiological processes, which restrict productivity in an environment, are often referred to as physiological limits. These limits can be overcome by modifying either the environment or the physiological characteristics of the crop, and the development of cultural practices and crop cultivars to exploit specific agricultural environments is a goal of agricultural research.

The study of physiological processes has traditionally concentrated on their response to environmental factors. However, there is increasing interest in the genetic control of plant processes and its potential for use in breeding programs. On theoretical grounds, it has often been suggested that independent selection and controlled recombination of individual physiological traits could be a valuable addition to the normal methods of plant breeding. The value of a physiological trait as a selection character depends, as do other selection characters, on whether it satisfies four basic criteria:

(a) There must be genetic variability in its expression. This variability must be of sufficient magnitude to justify the cost of assessing the character. Characters lacking a range of expression in the available germplasm may require new genetic technologies (Holl 1975) for their improvement.

(b) Its genetic control must be characterized. If selection for improved expression of a character is to be useful over a range of spatial and temporal environments, some stability of genotype performance (broad sense heritability) is necessary. In addition, the effective use of a character in a crossing program usually requires even more detailed information on the genetic systems involved, so that strategies for improvement can be formulated.

(c) It must be related to agronomic benefit. Agronomic benefit is a broad term which includes, in addition to yield, aspects of quality and production cost. Thus, even without yield increases, cultivars with higher protein content can increase the economic return from a crop, and legumes which derive a greater proportion of their nitrogen from symbiotic fixation, can decrease fertilizer costs. Nevertheless, the use of physiological characters is most often considered as a route to increased yield.

(d) It must be measurable in large-scale trials. While the first three criteria define the potential for use, practical exploitation will be impossible unless phenotypic expression can be assessed in large germplasm collections or segregating populations.

A physiological character can be defined as the measurable expression of the rate or duration of a physiological process. From this definition, a number of theoretical points about such characters and their applicability in selection programs follow. Physiological characters are hierarchical in the same sense as yield components. Figure 1, while in no way a comprehensive tabulation of all the yield limiting processes, illustrates how one series of char-

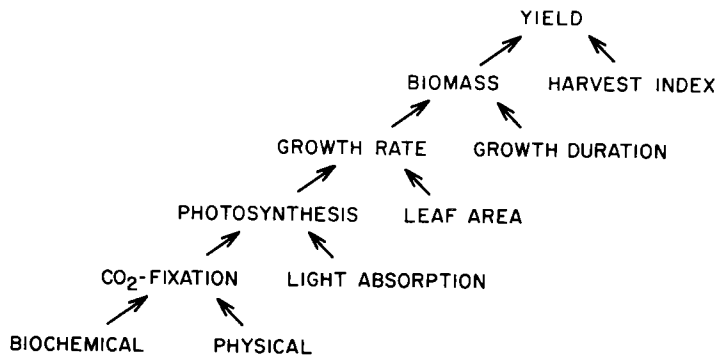

Fig. 1. Diagramatic scheme of the possible hierarchy in a number of physiological and yield characters.

acters might be related in such a hierarchy. A result of these causal relationships among physiological characters is that those near the output of the system will be more easily related to agronomically desirable traits, because there are fewer interactions with other processes, while those near the bottom will be more directly linked to initial gene products and more easily related to simple genetic control. Thus, resolution of both agronomic benefit and genetic control may be difficult to achieve for physiological characters.

Another corollary of the definition is that physiological characters are closely linked to morphology, not only because morphological changes are the end results of physiological processes, but because structures can themselves influence the rates. Morphological expression can be considered as a physiological or "morpho-physiological" character if it is assumed to control the rate of a process. Thus, the interest in flag leaf area of cereals (Simpson 1968; Yap and Harvey 1972; Apel et al. 1973; Borojevic et al. 1980) derives from the assumption that this area represents the major photosynthetic rate providing assimilates to the grain. Morphological expression can also be considered as physiological when it indicates the beginning or end of a process, as in the case of using black layer formation to indicate the end of seed ripening in corn (Daynard 1972).

A final aspect of physiological characters, defined in this way, relates to the variability which can be expected in their expression. Because of the exponential nature of the growth curve, large differences in final biomass can be caused by much smaller changes in the rate of a process which controls the relative growth rate. On the other hand, because physiological processes are sensitive to the environment, characters which depend on direct determination of rates are likely to be more variable than those which result indirectly from the integration of the rates of several processes over an extended time period. Thus, even if productivity were controlled absolutely by a single such character, its genetic variance is likely to be small and its error variance large, relative to those of final yield characters.

For a number of reasons, including those alluded to above, many believe that physiological characters do not meet any of the criteria for useful selection characters. Nevertheless, because agricultural productivity appears to be lower than we might theoretically expect (Tollenar 1983; Good and Bell 1980), physiological approaches are still recommended (Brown et al. 1975). In this review, the potential of physiolog-

ical characters for use in breeding programs is considered. As in the earlier and more comprehensive review by Wallace et al. (1972), this topic is organized in sections relating to the extent of genetic variability in physiological expression, its genetic control and the approaches which can be used to demonstrate its agronomic importance.

Genotypic Variability in Physiological Characters

There are numerous examples of simple genetic control of specific physiological processes. Some of these, such as the dwarfing genes in wheat (Austin et al. 1980), are already being exploited, while many others are deleterious or even lethal. Other well-studied physiological systems include those controlling flowering time, tolerance to stress and some aspects of disease resistance, each of which is a subject for an extensive review of its own.

The characters which have been less-well studied are those quantitative ones, which are difficult to measure, but which reflect processes controlling the growth of crop plants. While these characters may be the most difficult to include in selection programs, there is reason to believe that the prerequisite genetic variability does exist. Photosynthetic CO_2 exchange per unit of leaf area has been shown to vary considerably among genotypes of various crops measured in a single environment (Table 1). These results from both controlled environment and field measurements give an average coefficient of genotypic variability of 19%. Reports of genotype screening for a number of other continuously variable characters in several crop species have also shown considerable variation among the genotypes tested (Table 2). Some of these characters are related to photosynthesis and may even be the causes of the photosynthetic variability in Table 1. As well, however, growth rates and aspects of nitrogen metabolism had considerable genotypic variability. Symbiotic nitrogen fixation was most variable, perhaps because the rates reflect the genetic control of both nodulation and nodule activity and because of interactions with the bacterial genome. However, even the other characters in the table show an average genotypic CV of 16%.

Tables 1 and 2 include data from many sources, and the relative magnitude of the variability for these characters cannot be resolved. At the Prairie Regional Laboratory we have examined genotypic variability of seven physiological characters using 85 lines of peas (*Pisum sativum* L.) from a world pea collection, and have included four yield characters for comparison. The data from this single, replicated survey (Table 3) indicated significant ($P<0.05$) genotypic variability for all characters

Table 1. Genotypic variability in photosynthetic CO_2 exchange per unit of leaf area

Species	Number tested	Mean ($mgCO_2 \cdot dm^{-2} \cdot h^{-1}$)	CV† (%)	Reference
Zea mays L.	23	52	10	Duncan and Hesketh (1968)
	64	37	17	Crosbie et al. (1977)
Medicago sativa L.	35	53	26	Sheehy et al. (1980)
Glycine max (L.) Merr.	20	35	10	Dornhoff and Shibles (1970)
Helianthus annuus L.	47	40	41	Lloyd and Canvin (1977)
Triticum sp.	9	34	16	Evans and Dunstone (1970)
Phaseolus vulgaris L.	5	25	17	Kueneman et al. (1979)
	9	12	29	Peet et al. (1977)
Festuca arundinacea Shreb.	25	22	7	Asay et al. (1974)
Pisum sativum L.	25	25	17	Mahon and Hobbs (1981)
$\bar{X}$			19	

†CV is coefficient of variability based on genotype means from the published reports.

Table 2. Genotypic coefficients of variability for physiological characters

Character	CV† (%)	Reference
RUBP carboxylase	11	Peet et al. (1977), Frey and Moss (1976)
Specific leaf weight	10	Kueneman et al. (1979), Frey and Moss (1976), Dornhoff and Shibles (1970)
Stomatal resistance	20	Miskin et al. (1970), Dornhoff and Shibles (1970)
Photorespiration	28	Lloyd and Canvin (1977)
Photosynthetic area	17	Simpson (1968), Borojevic et al. (1980)
Relative growth rate	12	Jalani et al. (1979)
Relative leaf area growth rate	9	Duncan and Hesketh (1968), Apel (1979)
Seed growth	15	Cross (1975), Kaplan and Koller (1974), Johnson and Tanner (1972)
Duration of seed growth	18	Johnson and Tanner (1972)
Symbiotic N_2 fixation	52	Seetin and Barnes (1977), Wacek and Brill (1976), Zary et al. (1978)
Nitrate reductase	17	Deckard et al. (1973), Reed and Hageman (1980)
Nitrate uptake	26	Chevalier and Shrader (1977), Reed and Hageman (1980)

†Coefficients of variability (CV) were estimated from genotype means, and values represent the mean value for all cited reports.

studied. The yield characters of final biomass and seed yields showed a wide range of genotype means, whereas harvest index and seed nitrogen content were less variable. Among the physiological characters, rates of acetylene reduction, pod fill and estimated respiratory cost of fixation showed genotypic differences of magnitude similar to those of the final weight characters. Characters which might be expected to be related to the exponential growth constant such as photosynthesis, specific leaf weight, relative growth rate and root respiration were less variable across genotypes.

The data in Tables 1–3 indicate that ge-

Table 3. Variability in yield and physiological characters among 85 genotypes of peas grown in a single environment in Saskatchewan (all data were determined using field material grown in replicate blocks during 1979)

Character	$\bar{X}$	CV†	P‡
Yield			
Total weight ($g \cdot plant^{-1}$)	35	42	<0.001
Seed weight ($g \cdot plant^{-1}$)	16	32	<0.001
Harvest index (%)	50	18	<0.001
Seed nitrogen (%)	4.1	6	<0.001
Physiological			
Photosynthesis ($mgCO_2 \cdot dm^{-2} \cdot h^{-1}$)	20.3	10	<0.001
$N_2(C_2H_2)$ fixation ($\mu moles \cdot plant \cdot h^{-1}$)	6.4	35	<0.005
($\mu molc \cdot [g\ root]^{-1} \cdot h^{-1}$)	31.6	25	<0.01
Rate of pod fill ($mg \cdot day^{-1}$)§	48	25	<0.001
Root respiration ($\mu moles \cdot [g\ root]^{-1} \cdot h^{-1}$)	217	13	<0.05
Respiratory cost of fixation ($molesCO_2 \cdot [mole\ C_2H_2]^{-1}$)¶	3.1	29	<0.01
Relative growth rate (day^{-1})	0.15	13	<0.01
Specific leaf weight ($mg \cdot cm^{-2}$)	3.3	12	<0.05

†Coefficients of variability were estimated from genotype means.
‡Significance of genotype effects determined by analysis of variance.
§Based on 46 genotypes.
¶Estimated by the method of Hobbs and Mahon (1982a).

notype variability is a general property of physiological characters. However, many of these results are from controlled-environment studies, and even experiments with field-grown plants often used non-agronomic planting conditions to facilitate measurements. Because of this, there is concern that such estimates of genetic variability represent "potential expression", and that in agronomic conditions the genetic range of expression of a character or of its influence on plant growth may be absolutely limited by some other factor. Thus, genotypic variability might be reduced or have no relevance to plant performance in the field. There are specific examples, however, which demonstrate that this is not always the case.

Growth and photosynthesis were compared in genetic lines of peas which had been selected for extreme high and low rates of CO_2 exchange when grown under well-spaced conditions (Mahon 1982). Over 2 yr these genotypes were assayed for CO_2 exchange in wide-space plantings and also in dense stands, and equivalent growth rates were estimated for the stands. Photosynthetic CO_2 exchange rates were high and similar in the widely spaced plants in the 2 yr. However, the rates in stands were lower by 25% and 65% in the 2 yr. Despite this reduced rate of photosynthesis under simulated stand conditions, the genotypic differences in photosynthesis between the high- and low-selection groups remained proportionately the same. Moreover,in both cases the correlation across all genotypes between the photosynthetic rate and growth per unit of leaf area was highly significant.

A second example of expressed genotypic variability under both limiting and nonlimiting conditions is a study of acetylene reduction in soybean (*Glycine max* L. Merr.) cultivars by Wacek and Brill (1976). The rate of acetylene reduction varied greatly among the five cultivars with sucrose added to the medium. When sucrose was omitted, the rates were reduced by 50%, presumably because of a limiting supply of endogenous substrate. Nevertheless, even under these substrate-limited conditions, large differences were apparent among genotypes, although in this example, the ranking of the genotypes was altered.

These two examples show that genotypic variability persists even under conditions where the overall expression of a character is severely limited. Whether or not the relative performance of the genotypes is stable depends on the magnitude of the genotype × environment interactions and this question is more appropriately considered in the next section.

Genetic Control of Physiological Characters

The existence of significant genotypic variability in physiological characters suggests that there is scope for improving these characters by selection. However, variability within a single environment does not imply that selection will isolate genotypes with superior expression of the character over a range of environments. Physiological processes are known to be very sensitive to environmental conditions. Therefore, there is a danger that genotype × environment as well as main environment effects might be large. Such instability of genotype ranking would decrease the broad sense heritability (BSH) of the character and, thus, the efficiency of selection advance. In an earlier review, Wallace et al. (1972) suggested that BSH is close to 60% for physiological characters, and results from some more recent reports, where expression had been estimated in more than a single environment (Table 4), also indicate BSH to be between 35 and 75%. In those cases where more complete genetic studies have been carried out, estimates of narrow sense heritability (Table 4) indicated significant additivity, although values as low at 7% have been reported for photosynthetic CO_2 exchange. In our own studies, the physiological characters ex-

Table 4. Estimates of broad (BSH) and narrow (NSH) sense heritabilities for physiological characters

Character	Species	BSH (%)	NSH (%)	Reference
Photosynthetic CO_2 exchange	*P. vulgaris*	60	7	Wallace et al. (1976)
	Z. mays		58–80	Crosbie et al. (1977)
	F. arundinacea	65	25	Asay et al. (1974)
	P. sativum	75	65	Mahon and Hobbs (1981)
	G. max (canopy)	41–65		Harrison et al. (1981)
Stomatal frequency	*Hordeum vulgare* L.		27–74	Miskin et al. (1972)
RUBP carboxylase	*H. vulgare*	65		Frey and Moss (1976)
Specific leaf weight	*H. vulgare*	56		Frey and Moss (1976)
Flag leaf area	*H. vulgare*		49–66	Yap and Harvey (1971)
Growth rate	*Avena* sp.	38		Takeda and Frey (1977)
$N_2(C_2H_2)$ fixation	*P. sativum*		76–85	Hobbs and Mahon (1982b)

amined for 85 genotypes in a single environment (Table 3) have been further examined for 25 of the genotypes in two additional environments in a second year. The range of expression across all three environments, and estimates of BSH are presented for these same characters (Table 5). Final biomass and seed weights were greatly affected by environment, however, they had very high BSH values. Some physiological characters also had high BSH indicating that relative genotype performance was similar despite the environmental effects. In fact, the correlations across genotypes for photosynthesis, $N_2(C_2H_2)$ fixation, specific leaf weight and rate of pod fill were significant in all three comparisons of environments (unpublished results). Genotype means for root respiration were significantly correlated in two environments, but relative growth rates and respiratory cost of symbiotic nitrogen fixation showed no such stability of ranking, and the genotype effects were not significant over all these environments. Even including the values for these latter characters, however, the mean BSH for physiological characters was 65%. Combining this value with the average genotypic CV in a single environment (Table 3) of 20%, predicts that selection at an intensity of 5% should result in a genetic ad-

Table 5. Environmental variation and broad sense heritability of yield and physiological characters in 25 genotypes of peas†

Character	Range due to environment	Broad sense heritability (%)
Yield		
Total weight ($g \cdot plant^{-1}$)	9–35	94
Seed weight ($g \cdot plant^{-1}$)	3–13	93
Harvest index (%)	40–50	87
Seed nitrogen (%)	4.15–4.18	46
Physiological		
Photosynthesis ($mgCO_2 \cdot dm^{-2} \cdot h^{-1}$)	20–25	85
$N_2(C_2H_2)$ fixation ($\mu moles \cdot [g\ root]^{-1} \cdot h^{-1}$	4–26	80
Rate of pod fill ($mg \cdot day^{-1}$)‡	45–62	90
Root respiration ($\mu moles \cdot [g\ root]^{-1} \cdot h^{-1}$)	130–247	67
Respiratory cost of fixation ($molesCO_2 \cdot [moleC_2H_2]^{-1}$)	3.0–4.3	22§
Relative growth rate (day^{-1})	0.12–0.16	14§
Specific leaf weight ($mg \cdot cm^{-2}$)	3.3–3.6	93

†From Hobbs and Mahon (1982a).
‡Based on nine genotypes in the same three environments; manuscript in preparation.
§Genotypic variance not significant ($P<0.05$).

vance of approximately 26% of the mean (Allard 1960). Thus, there is reason to believe not only that genetic variability exists for physiological characters, but that genetic control is sufficient to allow improvement by selection, if there is any benefit to be gained by this genetic modification.

Determining the Relevance of Physiological Characters

Physiological characters are often difficult to measure. Because of their sensitivity to environment, large numbers of replications may be required to establish a meaningful value. In addition, some require destructive sampling and, thus, use up valuable plant material. These factors can be expected to add considerable cost to a breeding program, and a physiological character is not likely to be included unless there is convincing evidence that agronomic gains will be obtained. Unfortunately, there is no single method of unequivocally demonstrating the benefits of an individual physiological character. There are several experimental approaches to determining if a character is likely to be valuable; however, each has inherent weaknesses which should be considered.

(a) Examine the effect on performance of treatments which affect the character. For this approach environmental, chemical or physical manipulation can be used, as long as there is a known or measurable effect on the character, but the method requires absolute specificity of the treatment effect. As an example, an attempt to evaluate the importance of photorespiration by growing soybeans at low levels of O_2 clearly demonstrated increased vegetative growth; however, an independent effect on reproductive development virtually eliminated seed production, making yield comparisons meaningless (Quebedeaux and Hardy 1975). Inability to interpret treatment effects also arises if physiological compensation occurs. An example of this problem is the difficulty in determining the relative importance of different photosynthetic organs in cereals by using shading and excision techniques (Puckridge 1969). Finally, varying the expression of a character by environmental or physical manipulation may not affect growth in the same way as does genetic regulation of the character. Thus, in peas a twofold difference in photosynthetic rate from one year to the next resulted in a twofold difference in seed yield. Simultaneously, a 40% difference in rate between two groups of selected genotypes was not reflected in the seed yield in either year (Mahon 1982).

(b) Compare performance in isogenic lines. This method allows comparison of specific differences in physiological expression by genetic means, and has been used in evaluating the importance of a number of simply inherited traits. Epistatic effects may obscure the specific effects of varying the character. Thus, it is important that isogenic differences be tested in several genetic backgrounds, before generalized conclusions can be drawn about the effect of the specific character. Another drawback to this approach is that the polygenic nature of many quantitative characters may make the production of isogenic lines very difficult (Wallace et al. 1972).

(c) Compare performance by correlation. This is one of the most widely used methods, and it is based on the assumption that in a large sampling of genotypes, all characters other than the one of interest will be randomly distributed. The major difficulty in applying this technique to determine the effects of physiological characters is that assays may be too cumbersome to allow sufficiently broad sampling, and fortuitous correlations or correlations based on close genetic linkage may result. Even when data are based on large samples, physiological compensation remains a problem. In wheat, a highly significant relationship between flag leaf area and seed yield based on 143 genotypes does not necessarily allow the elimination of low leaf area types, since increased photosyn-

thesis per unit leaf area may enable such types to produce high grain yields (Apel et al. 1973).

(d) Examine evolutionary or breeding progressions for changes in expression. This approach assumes that selection, whether natural or controlled, will tend to accumulate desirable characters as populations become more adapted to their environments. Again, physiological compensation can be important as in the case of wheat in which modern hexaploid types exhibit decreased ability to assimulate CO_2 per unit leaf area, but increased leaf area (Evans and Dunstone 1970). Of greater importance is the possibility that natural selection might not adapt plants to optimal agronomic environments, and even in breeding programs, selection pressures might not be appropriate for selecting a particular physiological character. For example, nitrogen fixing ability of a legume might not even be expressed in selection program carried out on high nitrogen soils.

In general, it seems likely that the importance of any single physiological character will have to be inferred from the results of several experimental approaches. Moreover, there is no reason to believe that any one physiological process will be limiting crop performance to the same extent in all species or environments. Finally, it must be kept in mind that similar ends can be achieved by the exploitation of different physiological characteristics, as is the case in the hexaploid wheats which compensate for low rates of photosynthesis per unit leaf area by increased leaf area production (Evans and Dunstone 1970). For all of these reasons, the variability of physiological characters and the effects of this variability will have to be examined within the context of specific agronomic goals.

Summary

On the basis of the information now available, many physiological characters may be suitable for genetic manipulation. They can exhibit considerable genotypic variability in their expression, a high degree of stability in genotype ranking across environments, and in some cases a high narrow sense heritability, so that improvement through recombination and selection may be both effective and relatively straightforward. Thus, there is no reason to believe that the improvement of physiological characters is limited by either the genetic resources or the ability to exploit them using normal breeding methods. The major obstacle to using physiological characters for plant selection is an inability to demonstrate the agronomic importance of individual physiological characters. At present the lack of simple and rapid methods for determining physiological expression prevents the inclusion of these characters in the very programs which could produce the genetic material needed to examine their relevance. Both improved methodology and an increased appreciation of the genetic diversity in physiological characters will be needed to overcome this obstacle.

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