

Combining ability for components of resistance to early leaf spot and yield of inter- and intraspecific peanut lines*

M. OUEDRAOGO,
O.D. SMITH, corresponding author,
Dept. of Soil and Crop Sciences, Texas A&M
University, College Station TX 77843,

C. E. SIMPSON,
Texas Agricultural Experiment Station,
Stephenville TX 76401,

B. BESLER,
Texas Agricultural Experiment Station,
Yoakum TX 77995

Abstract : Seven interspecific peanut lines and the cultivar «Southern Runner» were crossed in a half-diallel, i.e. without reciprocals. F_1 plants were selfed and F_2 progenies evaluated for early leaf spot reaction and yield. The purpose of the study was to ascertain from F_1 and F_2 populations, crosses which were most likely to give the greatest expression of early leaf spot resistance and yield. Field early leaf spot assessment was made using the Florida leaf spot rating scale and determinations were made for lesion diameter, amount of sporulation, and latent period in both the field and laboratory. Genetic analysis was performed using the Griffing method 2 model 1. Significant differences existed among crosses for visual leaf spot rating, latent period, and amount of sporulation in the F_2 generation ($P=0.05$). Pod yield, based on individual plants, differed significantly ($P=0.05$) among the F_2 progenies but not in the F_1 . Little heterosis was found among the F_1 hybrids. Performance in the F_1 was not reflected in the performance of the F_2 as rank correlation between the two populations for pod yield was low ($r=0.32$) and not significant ($P=0.05$). Combining ability effects (both general and specific) were significant for yield and disease parameters in the F_2 generation.

Key-words: *Arachis hypogaea*, peanut, groundnut, *Cercospora arachidicola*, *Cercosporidium personatum*, introgression, interspecific lines, diallel, combining ability.

Introduction

Early Leaf spot caused by *Cercospora arachidicola* Hori is a very important disease of peanut. Porter *et al.* (1982) reported that it occurs wherever peanut is cultivated. The preferred means of managing this disease would be the growing of resistant peanut cultivars. However, the partial resistance in current cultivars is inadequate for total disease management without fungicides. Success in developing agronomically desirable varieties resistant to the early leaf spot fungus has been limited.

The development of improved leaf spot resistant varieties is hampered by a tight linkage between high yield and susceptibility or pleiotropism (Iroume and Knauff, 1987). Introgression of early leaf spot resistance from the wild species to the cultivated has been accomplished using different procedures (Simpson, 1991, Stalker, 1984). Utilization of wild species is tedious with only limited success, furthermore lines with early leaf spot resistance have the disadvantage of reduced yield. In previous studies, Ouedraogo (1990) found that: 1) none of the introgressed lines in the Texas peanut breeding Program at Texas A&M with reasonable agronomic acceptability had leaf spot resistance equivalent to the parental wild species, and 2) the introgressed lines that had the best combinations of agronomic traits and leaf spot resistance have variability for genes controlling the disease components of interest (lesion diameter, latent period, and amount of sporulation). Since leaf spot is quantitatively inherited, interspecific lines with

partial resistance to the disease might be homozygous for different resistance genes. Hybridization and selection potential among lines with different genetic background and partial resistance to early leaf spot might provide information of tremendous importance to peanut breeders.

The objective of this study was to evaluate the potential for recombining genetic factors controlling early leaf spot resistance and desirable agronomic characters in selected lines partially resistant to early leaf spot. The goal is to select *hypogaea*-like breeding lines with good agronomic traits and high concentrations of early leaf spot resistance.

Materials and methods

Five interspecific ($2n=40$) lines for which parentage included *Arachis* species *cardenasii*, *diogeni*, *batizocoi* and *hypogaea* subspecies *hypogaea* and *fastigiata*, (Simpson, 1991) two interspecific lines from ICRISAT, and one intraspecific cultivar («Southern Runner») were crossed in a half diallel, i.e. without reciprocals. The derivation of the five interspecific lines is shown in figure 1. The ICRISAT materials were derived by a direct cross between *A. cardenasii* and *A. hypogaea* using the hexaploid route. The eight parents were tested in 1990 and were subsequently included in experiments designed to evaluate their F_1 and F_2 progenies. Ten F_1 seed per cross from the 28 single crosses were planted in the field in summer 1991 and in 1992 in a randomized complete block design with two replications. The F_1 plants from the 1991 test were harvested individually, and the F_2 seed bulked within a cross and planted in a completely randomized design field test with three replications. Experiments for the F_1 generations were conducted at Bryan Texas in sandy loam soil. The F_2 populations were tested at the Texas Agricultural Research Station near Yoakum in a loamy fine sand soil on a site that had been planted to peanut the two previous years. Leaf spots were a recurrent problem at the test site and disease infected residue, although moldboard plowed into the soil, gave rise to leaf spot infection in most years.

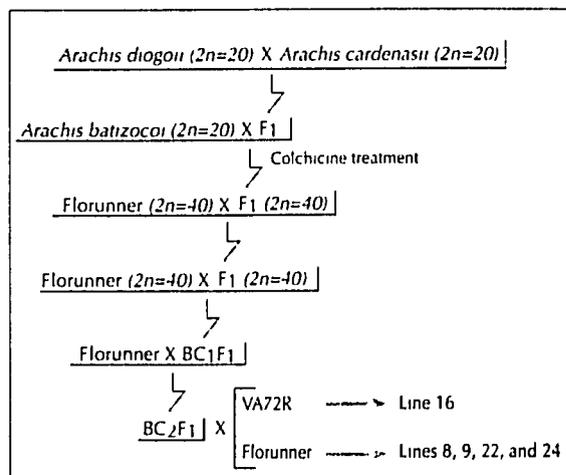


Figure 1 Derivation of the five interspecific lines by the bridge cross breeding scheme for introgression of pest resistance into cultivated species of peanut.

Cultural practices were in accordance with those recommended for irrigated peanut production in Texas with the exception of fungicidal disease management. Weeds were controlled with pre-plant incorporated trifluralin (1.7 L ha^{-1}) and metachlor (1.8 L ha^{-1}). No insecticide was required. Plots were harvested when most entries were considered mature on the basis of vine appearance.

Individual F_1 plants were assessed at 110 and 130 days after planting (DAP) for disease reaction using the Florida Scale (Chiteka *et al.*, 1988). This scale is visual and ranges from 1 (no disease) to 10 (plant dead) on the basis of the whole plant appearance after natural inoculation with the pathogen. Lesion diameter, amount of sporulation, and latent period were also determined on individual plants in the field as follows: three non-diseased leaves were tagged per plant in the field at 30 DAP.

Table 1. Average reaction to *C. arachidicola* and yield of parental lines

Entry	FSR*	Latent period (days)	Lesion diameter (mm)	Amount of sporulation*	Pod (g/plant)	Seed	20 seed weight (g)
Line 9	5.3	27	3.1	1.50	75.2	60.2	12.4
Line 22	6.2	23	3.6	1.50	76.4	58.5	12.3
Line 24	6.1	18	3.1	1.50	77.9	60.4	12.8
Line 8	3.5	35	3.2	1.49	53.6	38.7	12.4
Line 16	2.8	11	2.6	1.50	67.6	47.6	12.3
ICRISAT CS-39	3.6	26	2.5	1.47	32.2	19.4	10.8
ICRISAT 104	4.1	25	2.7	1.50	47.2	30.8	9.0
So Runner	5.5	21	2.8	1.50	94.1	75.3	12.0
LSD 5%	0.8	8	0.4	0.06	41.7	31.8	2.6

*FSR=Florida Scale Rating at 130 days after plant.

* Visual scale: 0=no sporulation, 5=maximum sporulation

2

(prior to the appearance of any lesion). Leaves were examined every other day to determine the date of appearance and the day of sporulation of the lesions visually under 20X magnification. When sporulation was observed, the greatest diameter of the lesion was measured using a ruler and the amount of sporulation estimated using a scale ranging from 0 (no sporulation) to 5 (maximum sporulation). The latent periods reported in this study were, therefore, the number of days between the appearance of the lesion and its first sporulation. Pod and seed yields of individual F₁ plants were determined by weight. Disease assessment was performed and plant yield was recorded on individual F₂ plants as on the F₁. Each plot consisted of a single row of 25 plants. All data collected were analyzed using ANOVA. Diallel analyses were performed from the F₁'s, F₂'s, and parents using leaf spot data and single plant yield. The combining ability analyses were conducted when the entry mean squares were significant according to the F test on the ANOVA table. General combining ability (GCA) and specific combining ability (SCA) effects were determined according to Griffing method 2 model 1 (1956) which was most appropriate in our situation since parents were selected on the basis of past performance and were considered fixed. One set of crosses and the parents were included in the analysis. The relative importance of GCA and SCA effects was estimated using the ratio $r = 2MS_{GCA} / (2MS_{GCA} + MS_{SCA})$ (Baker, 1978). Additive gene effects are of primary importance when this ratio is close to unity.

Results

Parental performance

Parents used in the study were tested in 1990 for both disease reaction and yield (table 1). Significant differences (p=0.05) were found for early leaf spot based on the FSR, latent period, lesion diameter, and amount of sporulation. Southern Runner, and ICRISAT CS-39 had the smallest lesion diameters. Line 8 had the longest latent period

and line 16 the shortest. Very little variability was found for amount of sporulation.

Pod yield ranged from 32.2 g/plant for ICRISAT CS-39 to 94.1 for Southern Runner (table 1). Both pod and seed yields were low for the ICRISAT material. Seed yield and seed weight for the ICRISAT parents make them unsuitable for the American market. These two lines also had the lowest 20 seed weight of all the parents. In addition, ICRISAT 104 pods were very difficult to shell and the seed were irregular in shape.

In this preliminary evaluation, the chosen parents, except for the two lines from ICRISAT, had pod yield and grading characteristics comparable to Southern Runner. The use of the ICRISAT material might cause a challenge when selecting for good agronomic characters in their progenies.

Combining ability for disease trait

No differences were found among F₁ families for early leaf spot parameters. However, in the F₂ generation, significant differences occurred among crosses in leaf spot reaction using the Florida scale rating (FSR) at 130 DAP, lesion diameter, latent period, and amount of sporulation. This allowed the partition of the variation due to crosses into GCA and SCA effects (table 2).

General and specific combining ability effects were significant for latent period, lesion diameter, FSR at 130 DAP, and amount of sporulation. Lesion diameter, and FSR at 130 DAP were controlled primarily by additive gene effects as suggested by the ratio of GCA to SCA (table 2). This is an indication that breeding methods that take advantage of additive types of gene action should be effective for these two traits.

For FSR at 130 DAP, Southern Runner had a significant, positive effect, suggesting that it contributed to greater susceptibility in its F₂ progenies (table 3). This is not surprising since most of the leaf disease symptoms were typical of early leaf spot, to which Southern Runner is susceptible. In general, Southern Runner and ICRISAT 104 transmitted a short latent period to their F₂ progenies, while line 8 transmitted a

Table 2. Mean squares for general and specific combining abilities for parameters of resistance to *C. arachidicola* measured on the parents and their F₂ generation progenies planted in the field at Yaokum 1992

Source of variation	Df	Mean squares			
		FSR*	Latent period	Lesion diameter	Amount of sporulation
Entries	35	2.31**	66.98**	0.61**	0.075**
GCA	7	8.03**	96.64**	1.59**	0.0729*
SCA	28	0.88**	59.57**	0.36**	0.076*
Error	63	0.22	16.52	0.09	0.03
r [†]		0.95	0.76	0.90	0.65

Error Df for latent period was 516 and error Df for lesion diameter and amount of sporulation were 693.

* significant at P=0.05

** significant at P=0.01

† ratio of GCA to SCA as per Baker, (1978)

‡ FSR=Florida Scale Rating at 130 days after plant

long latent period to its progenies (table 3) Line 16 contributed to the reduction of the lesion diameter in its progenies, while lesion size was increased by lines 9, and 22, and Southern Runner.

The coefficient of correlation between parental GCA and performance *per se* ($r=0.98$) was significant at $p=0.01$ for the FSR at 130 DAP. This indicates that parental GCA was in agreement with performance *per se* and that among these lines, superior parents for early leaf spot resistance could be selected based on the reaction of the lines. In contrast, parental GCA for latent period and lesion diameter were not predictable based on performance *per se* since the correlation coefficients were 0.46 and 0.69 respectively, and were not significant ($p=0.05$) GCA effects for lesion diameter and the FSR at 130 DAP were significantly ($p=0.05$) correlated ($r=0.74$) This suggests that selection for one trait should result in gain for the other and vice versa. SCA estimates (not shown) were small and mostly non-significant for

lesion diameter, FSR, and amount of sporulation. Significance of the SCA estimates for latent period suggest that the SCA effects play a more important role in this trait ($r=0.76$).

Yield and seed size

Both GCA and SCA effects were found for pod and seed yield and seed size in the F_1 and F_2 progenies (table 4) The general effect of parents on progeny was greater than the specific effect, larger on pod as compared to seed, and greater on F_2 than F_1 generation progeny as revealed by the ratios calculated following the procedure of Baker (1978) Southern Runner had a consistent positive contribution on both pod and seed yield in both generation progenies (table 5) The effects of other parents were either moderate or inconsistent. Notable, although not always significant ($P=0.05$), effects were found such as the positive

Table 3. Estimates of general combining ability effects for parameters of resistance to *C. arachidicola* for the F_2 field evaluation at Yoakum 1992

Entry	FSR *	Latent period	lesion diameter	Amount of sporulation
Line 9	0.13	2.05	0.27*	-0.002
Line 22	0.65**	0.05	0.29*	0.012
Line 24	0.62**	-1.55	0.19	-0.005
Line 8	-0.63**	3.75*	0.20	0.004
Line 16	-0.72**	0.45	-0.30*	0.001
ICRISAT CS-39	-0.37**	2.05	-0.11	-0.009
ICRISAT 104	-0.21	-3.65*	-0.04	0.004
So Runner	0.53**	-3.15*	0.43**	-0.005
SE	0.12	1.62	0.13	0.08
LSD 5%	0.24	3.18	0.25	0.16
LSD 1%	0.32	4.17	0.33	0.20

* significant estimates at $P=0.05$

** significant estimates at $P=0.01$

‡ FSR=Florida Scale Rating at 130 days after plant

Table 4. Mean squares for general and specific combining abilities for three yield characters measured on the parents and their F_1 and F_2 generation progenies planted in the field at Bryan and Yoakum, respectively, in 1992.

Source of variation	Df	Mean squares					
		Pod yield		Seed yield		20 seed weight	
		F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
Rep	2	988.17	753.77	691.60	574.16	0.67	0.04
Entries	35	1835.82**	610.71**	1120.31**	407.46**	3.37**	3.88**
GCA	7	1714.43**	894.70**	1668.18**	837.06**	3.81*	13.84**
SCA	28	1866.16**	539.71*	983.35**	299.54*	2.91*	1.39*
Error	32	386.58	288.97	224.70	180.74	1.37	0.71
r^{\ddagger}		0.65	0.77	0.77	0.85	0.78	0.95

* significant at $P=0.05$

** significant at $P=0.01$

‡ ratio of GCA to SCA as per Baker, (1978).

- 4 -

effect of line 24 and negative effect of line 16 on hybrid but not F_2 pod and seed yields. ICRISAT 104 tended to cause lower than average seed yields for both F_1 and F_2 progeny. For seed size, the result showed more of a general over cross combination, rather than a specific by cross effect of parents, especially in the F_2 generation offspring, in which the ratio of GCA to total entry variance was 95%. Examination of individual parents for contribution to the overall GCA shows a consistent, over generation, influence of ICRISAT 104 toward small seed. None of the other parents produced an effect different from the average in the hybrids, although in the F_2 the influence of lines 8 and 24 were for larger than average seed. The two ICRISAT lines had negative GCA estimates for both pod and seed yield. ICRISAT 104 had the lowest GCA for pod and seed yield and 20-seed weight. ICRISAT CS-39 was the second poorest except for pod yield.

Discussion

General combining ability accounted for most of the entry variation for disease resistance, as measured by the Florida Scale, in the F_2 generation progenies of these eight parents. Non-additive, presumably dominance, effects in the F_2 on the ratings, which might confound selection, were small. Thus, selection for leaf spot reaction at this early generation should be effective.

The components of disease resistance were studied to determine if these inter- and intraspecific derived parents differ in components which might contribute to a higher expression of resistance in their common offspring. Differences among parents were confirmed (table 1). Transmission of the differing components of resistance from these parents to their offspring was mostly additive in effect as measured by F_2 progenies. However, non-additive (perhaps dominance) effects were more prominent for some components than others: amount of sporulation > latent period > lesion size (diameter), and the variance

among parents for amount of sporulation was small. Selection among F_2 progenies for lesion diameter would seem more effective than for the other two components. The effectiveness of selection for latent period might be enhanced by delay until a later generation when heterozygosity and dominance expression is reduced from that in the F_2 .

The result that GCA effects were higher for the overall plant appearance score as compared to individual component scores, especially latent period and amount of sporulation, is baffling. Latent period as measured for natural infection is tedious and laborious to determine, and determining the amount of sporulation is highly subjective. In this study data on latent period were collected over a 50-day period of time, thirty to 80 days after planting. Lesion diameter and amount of sporulation were recorded the first day sporulation was noticed. It is not known whether lesion diameter would increase after sporulation started. Amount of sporulation on the other hand is highly affected by the environmental conditions (Alderman and Beute, 1987) which is expected to vary in a field considering the extended period of time the data was collected. The possibility of error as to the appropriate date of assessing the components of disease resistance cannot be discounted. Selection in early generation would be most effective with the FSR than the individual components of disease resistance. In addition, no parent contributed significantly to more than one component of disease resistance. The significant correlation between FSR and lesion diameter suggests that selection for one trait should result in gain for the other and vice versa. This result is similar to the finding of Chitika *et al* (1988) who reported a positive and significant correlation between FSR and lesion diameter at 135 DAP for late leaf spot. In respect to disease resistance as measured by the FSR, parents with good performance had good GCA and produced offspring favorable for selection. Thus, a logical conclusion for breeding is to select as parents the candidates with the best performance. For important traits such as FSR, the goal is to find the most elite genotypes. Specific com-

Table 5 Estimates of general combining ability effects for yield characters measured on the parents and their F_1 and F_2 generation progenies planted in the field at Bryan and Yoakum, respectively, in 1992

Entry	g/plant					
	Pod		Seed		20 Seed weight	
	F_1	F_2	F_1	F_2	F_1	F_2
Line 9	-4.15	-1.02	-3.99	2.19	-0.01	0.003
Line 22	5.27	-2.89	5.45	-1.87	0.18	0.003
Line 24	10.48	-2.96	10.05*	0.74	0.43	0.603*
Line 8	-3.79	5.71	-4.25	4.26	0.31	0.753*
Line 16	-8.08	-0.31	-9.13*	-1.08	-0.11	0.423
ICRISAT CS-39	-8.41	-2.04	-6.79	-3.77	0.25	-0.228
ICRISAT 104	-7.31	-7.75	-7.26	-9.71**	-1.27**	-1.998**
So Runner	16.01*	10.63*	15.92**	9.23**	0.24	0.433
SE	6.21	4.39	4.74	3.47	0.37	0.27
LSD 5%	12.66	8.78	9.67	6.94	0.75	0.54
LSD 1%	17.08	11.68	13.04	9.23	1.02	1.44

* significant estimates at $P=0.05$

** significant estimates at $P=0.01$.

binning ability was found which, if a function of epistasis rather than dominance, suggest that superior parental combinations might be found. Whether the SCA resulted from better than predicted performance among parents with high GCA is unknown. In this test, the cross with the lowest FSR derived from line 8 x ICRISAT 104. Both of these parents had negative GCA values, but the effect of ICRISAT 104 was not significant. Other parental combinations where both parents expressed highly significant negative GCA produced progeny with higher disease ratings than these. Similar reports were found for yield on peanut but not for disease. Upadhyaya *et al* (1992) reported that the majority of the best specific combinations for different yield characters in peanut resulted from crosses among parents with high by low or low by low GCA effects.

The proportion of entry variation that was non-additive was greater for pod and seed yield than for FSR and lesion diameter. Dominance effects were involved in yield as indicated by the increase in the GCA to SCA ratio for the F₂ as compared to the F₁ generation data. Thus, delay in the selection of populations for yield until the F₂ or later generations would seem most effective. Anderson *et al* (1993) reported the predominance of GCA and the presence of modifier genes in peanut yield.

Non-additive variance as indicated by significant SCA is also apparent in the inheritance of seed size. The notable increase in the ratio of GCA to SCA determined from the F₂ compared to the F₁ generation populations indicates that dominance effect was an important factor in the hybrids. The rapid increase in the GCA SCA ratio from one generation of self-pollination also is indicative of the simpler inheritance of seed size as compared to yield.

The ultimate goal of the study, of which this is a part, is to identify populations and eventually lines with a high level of early leaf spot resistance that produce high yield and acceptable seed size using the introgressed germplasm. The GCA estimates for yield for Southern Runner were consistently high over the F₁ and F₂ generations. As expected, the improvement for pod and seed yield will be highest within the progenies of Southern Runner as compared to the interspecific lines. Based on the F₂ data, ICRISAT CS-39 contributed positively to lower FSR in its progenies while ICRISAT 104 contributed to a shorter latent period in its progenies. However these lines also ranked as the most negative in the general combining ability estimates for yield and seed weight. Therefore, it may be speculated that this material represents a slightly different gene pool for yield character although very little heterotic effect is produced. Arunachalam *et al.* (1984) reported that the magnitude of heterosis for yield and its components in peanut were higher in crosses between the parents in intermediate divergence classes than in the extreme ones.

Overall there was no correlation between disease parameter and yield whether using *per se* performance or general combining ability. This

implies that successful selection for the elite in both disease resistance and yield will require a careful attention to both traits in this germplasm. However, some encouragement was gained because negative correlation between disease resistance and yield was not found as previously reported by Iroume and Knauff (1987). Nevertheless, the true test must derive from the disease reaction and yield of later generation progeny. Such studies are now in progress.

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• Supports matériels

Le manuscrit doit être dactylographié, en double interligne, uniquement au recto, chaque page numérotée et accompagnée par les figures et les tableaux. Les mots de lignes à apparaître en italique doivent être soulignés.

Chaque manuscrit doit être adressé dactylographié et accompagné d'une saisie sur disquette éditée de préférence en Word et portant les indications suivantes : titre exact du fichier, nom du système d'exploitation (ex. MS DOS, Apple, Unix). Si le logiciel le permet les enregistrements seront effectués en format «texte» ou «ASCII». Les tableaux doivent être enregistrés dans un fichier séparé.

• Page de titre

La page de titre doit indiquer : (1) le titre en français, court, spécifique, informatif et comprenant un ou deux mots clés destinés à l'indexation ; (2) le titre courant (maximum 50 caractères) ; (3) le prénom de(s) l'auteur(s) suivi de son nom ; (4) l'adresse de(s) l'auteur(s) comprenant le service,

l'institution, la ville, le code postal et le pays. L'auteur auquel la correspondance sera adressée doit être indiqué, et son adresse doit inclure ses numéros de téléphone et de télécopie.

• Références

Les références bibliographiques doivent être numérotées dans l'ordre d'apparition dans le texte, appelées dans le texte par un numéro placé entre crochets. Lorsque le nombre des auteurs est inférieur à 6 tous les noms sont indiqués. Lorsqu'il y en a 7 ou plus, indiquez les noms des trois premiers suivis de *et al*.

Les références comprendront dans l'ordre suivant : les noms suivis des initiales des prénoms des auteurs, l'année, le titre de l'article, le titre du journal abrégé selon les normes internationales indiquées dans la liste mondiale des périodiques scientifiques, le volume, les 1^{ère} et dernière pages, ainsi que le nom et la ville de l'éditeur dans le cas des livres. Les références doivent ainsi être présentées de la manière suivante :

1. CRAIGEN WJ, CASKEY CT (1987) Translational frameshifting where will it stop ? *Cell*, 50 1-2.

2. NEILANDS JB (1974). Iron and its role in microbial physiology. In : *Microbial iron metabolism*, JB Neilands, ed. New York Academic Press, 3-34.

3. MILLER JH (1972) *Experiments in molecular genetics*. Cold Spring Harbor, New York. Cold Spring Harbor Laboratory Press.

• Figures

Un jeu de photographies, ou de figures obtenues avec une imprimante de bonne qualité, ou de documents originaux, doit être fourni pour la reproduction des figures. Les photographies doivent si possible être des documents originaux. Si possible, les figures doivent être soumises dans leur format final. Aucun document original ne doit dépasser, à l'exception de certains clichés radiologiques, le format A4 (21 x 29,7 cm).

• Conventions et abréviations

Les abréviations doivent être définies entre parenthèses lors de leur première citation dans le texte. Les unités, les symboles et la nomenclature doivent respecter les conventions internationales. Les unités, de mesure standard et les symboles d'éléments chimiques seront utilisés sans être définis dans le manuscrit.

CORRECTION DES AUTEURS

Les articles préparés avant impression, seront envoyés aux auteurs et devront être relus avec soin et renvoyés à l'éditeur sous 48 heures par courrier ou par télécopie.

À PARAÎTRE :
LES PROCHAINS DOSSIERS DE OCL

- Oléagineux, pays du Sud et développement (2, 3)
- Qualité et assurance qualité (2, 4)
- Lipochimie : présence et prospective (2, 5)
- Oléagineux et environnement (2, 6)