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Genetic variability in photosynthetic rate and leaf characters in *Brassicaceae* coenospecies

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Abstract

Thirty-nine *Brassica* coenospecies grown in pot cultures during 1993 and 1994 were screened for variability in photosynthetic rate (P_N) and leaf characters. There were significant differences among the species in P_N per unit leaf area, chlorophyll (Chl) content, specific leaf mass (SLM), stomatal resistance (r_s) and individual leaf size. The interactions species × year and species × date of measurement were small compared to the species effect. There was a significant negative correlation between P_N and r_s and a significant positive one between P_N and both Chl content and SLM.

Additional key words: *Brassica*; chlorophyll content; leaf area; specific leaf mass; stomatal resistance.

Introduction

The P_N improvement in crop plants may result in increased biological and economic yield (Zelitch 1982). Genetic variability for P_N is a prerequisite for the selection of genetically superior types for this character (Criswell and Shibles 1971). Such variability exists in several crops such as wheat (Evans and Dunstone 1970, Austin *et al.* 1982), maize (Heichel and Musgrave 1969) and soybean (Buttery *et al.* 1981). Cultivated germplasm is likely to be less genetically diverse than wild germplasm because of founders effect whereby only a small portion of the genetic diversity of a species is carried onto the cultivated germplasm during domestication (Lynch *et al.* 1992). *Brassica* coenospecies including wild germplasm represent a potential genetic source of improvement of traits related to leaf photosynthesis in cultivated *Brassica*.

Variability in P_N is associated with r_s (Dornhoff and Shibles 1970, Hobbs and Mahon 1985, Janssen *et al.* 1995), SLM (Pearce *et al.* 1969, Dornhoff and Shibles 1970, Hesketh *et al.* 1981), leaf size (Bhagsari and Brown 1986) and Chl content

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(Buttery and Buzzell 1977, Hobbs and Mahon 1985). However, correlations between the characters are not always the same for all species and under all conditions. Therefore it is important to determine the relationships among leaf characters for each crop. Information with regard to leaf photosynthesis and related parameters is scarce in *Brassica* coenospecies. In the present study thirty nine coenospecies of *Brassica* were screened to determine the variability in P_N and other associated leaf characters.

Materials and methods

Thirty-nine *Brassicaceae* coenospecies representing different genera (Table 1) were raised in earthen pots (35 × 40 cm) containing sandy-loam soil, under natural conditions. Three plants were maintained per pot and one plant in each pot was marked for observations. Top most fully expanded leaf of the marked plants was selected from three different pots to measure P_N and r_s using portable Infra Red Gas Analyzer model *LI-6000* (*LICOR,* U.S.A.). The leaf was immediately excised and measured for total leaf size as well as the portion enclosed in the chamber, with the help of leaf area meter (*Hayashi Denko,* Japan). A representative sample was then taken for estimating Chl content as described by Hiscox and Israelstam (1979). The remaining material was dried at 75 °C for 48 h for dry mass and SLM determination. The SLM was calculated based on the leaf area and leaf dry mass measurements. Eight samplings were done at different growth stages between 30 to 152 d after planting. All the above measurements were carried out on cloudless days. There were, invariably, three replications for each determination. The values obtained for various parameters were tested by analysis of variance, Duncan's Multiple Range Test and correlations following standard methods (Gomez and Gomez 1984) and *MICROSTAT* software, were developed by H.J. Barreto and W.R. Raun, CIMMYT, Mexico.

Results and discussion

Among the *Brassica* coenospecies studied, a significant variability in P_N existed (Table 1). The mean P_N ranged from 9.4 to 27.3 μmol(CO_2) m^{-2} s^{-1}. The highest P_N was recorded in *B. catholica* and the lowest one in *Camelina sativa.* Such large variability was also in conformity with the findings of Buttery *et al.* (1981) in soybean. Cultivated species of *Brassica* showed lower rates compared to the wild species. Similarly, the highest P_N has been recorded for wheat, sorghum, pearl millet and cotton in wild species (Gifford and Evans 1981). Differences among species for similar leaf characters are mainly related to ploidy level in wheat (Austin *et al.* 1982). Our study showed that, of the two *B. gravinae* species differing in ploidy, the tetraploid exhibited higher P_N than the diploid.

Amid 39 species, the mean SLM ranged from 23 in *B. tournefortii* to 65 g m^{-2} in *B. pubescens* (Table 1). A positive significant correlation existed between P_N and

SLM (Table 2, Fig. 1) which was in conformity with Dornhoff and Shibles (1971) in oats. Bhagsari and Brown (1986) suggest that the variations in P_N are mainly due to

Table 1. Seasonal means of net photosynthetic rate (P_N) [µmol(CO$_2$) m^{-2} s^{-1}], chlorophyll (Chl) content [mg m^{-2}], stomatal resistance (r_s) [s cm^{-1}], specific leaf mass (SLM) [g m^{-2}], and leaf size (A) [cm^2] in *Brassica* coenospecies. Means within a column followed by the same letter are not different at the 0.05 probability level according to Duncan's multiple range test.

Species	r_s	P_N	Chl	SLM	A
1 *Brasica tournefortii*	0.374^{jklmn}	19.6^{efghi}	$44.9^{efghijkl}$	29^{ij}	42.5^{cde}
2 *B. tournefortii* (local)	$0.389^{hijklmn}$	21.7^{cde}	$41.3^{fghijklmno}$	$41^{defghij}$	28.6^{fghijk}
3 *B. cossoniana*	0.379^{hijklm}	23.7^{bc}	$40.2^{ghijklmno}$	36^{efghij}	30.1^{fghijk}
4 *B. maurorum*	0.403^{hijklm}	19.4^{efghi}	$45.4^{efghijk}$	$41^{defghij}$	19.6^{klmnop}
5 *B. fruticulosa*	0.374^{ijklmn}	20.8^{def}	$44.8^{efghijklm}$	$42^{defghij}$	21.2^{klmnop}
6 *B. fruticulosa* (Spain)	0.628^{bcdef}	17.7^{ghijk}	$42.6^{efghijklmn}$	55^{abcd}	25.3^{ijklmn}
7 *B. oxyrrhina*	0.402^{hijklm}	18.6^{fghij}	59.4^{ab}	59^{abc}	57.9^{a}
8 *B. barrelieri*	$0.424^{ghijklm}$	16.6^{jklmno}	58.8^{abc}	48^{bcdefg}	54.6^{ab}
9 *B. spinescens*	$0.579^{bcdefgh}$	14.3^{opq}	55.5^{abcd}	59^{abc}	14.9^{nop}
10 *B. gravinae* (diploid)	$0.435^{fghijklm}$	15.1^{lmnop}	34.7^{lmnopq}	36^{efghij}	20.5^{klmnop}
11 *B. gravinae* (tetraploid)	$0.383^{hijklmn}$	16.7^{jklmn}	$47.1^{defghij}$	51^{abcde}	16.1^{mnop}
12 *B. juncea*	0.755^{ab}	17.7^{hijk}	30.1^{pqr}	$40^{defghij}$	45.1^{bcd}
13 *B. campestris*	0.704^{bc}	16.0^{klmnop}	$37.7^{ijklmnopq}$	32^{hij}	27.5^{ghijkl}
14 *B. napus*	0.607^{bcdefg}	17.3^{ijkl}	$37.3^{jklmnopq}$	27^{j}	44.5^{cde}
15 *Diplotaxis mualis*	0.264^{lmn}	19.3^{efghi}	$46.5^{defghij}$	45^{cdefgh}	14.3^{nop}
16 *D. harra*	0.344^{klmn}	17.9^{ghijk}	31.3^{opq}	36^{efghij}	17.1^{lmnop}
17 *D. siettiana*	$0.386^{hijklmn}$	24.2^{b1}	$40.4^{ghijklmno}$	64^{a}	20.7^{klmnop}
18 *D. berthautii*	$0.428^{ghijklm}$	20.5^{def}	$37.9^{ijklmnopq}$	39^{efghij}	20.0^{klmnop}
19 *D. catholica*	$0.389^{hijklmn}$	27.3^{a}	63.1^{a}	62^{ab}	14.1^{op}
20 *D. erucoides*	$0.464^{efghijkl}$	22.4^{bcd}	$43.6^{efghijklmn}$	$41^{defghij}$	35.9^{defghi}
21 *D. assurgens*	0.406^{hijklm}	20.2^{defg}	$40.4^{ghijklmno}$	37^{efghij}	34.1^{efghij}
22 *D. cretacea*	0.376^{ijklm}	17.2^{ijkl}	34.5^{mnopq}	35^{fghij}	30.6^{fghijk}
23 *D. siifolia*	$0.472^{defghijk}$	17.4^{hijkl}	$43.0^{efghijklmn}$	$42^{defghij}$	38.5^{def}
24 *D. tenuifolia*	$0.424^{ghijklm}$	17.7^{ghijk}	$42.0^{efghijklmn}$	35^{fghij}	37.8^{defg}
25 *D. viminea*	0.370^{jklmn}	12.5^{qr}	22.0^{r}	33^{hijkl}	11.1^{p}
26 *Camelina sativa*	$0.494^{defghijk}$	9.4^{s}	28.2^{qr}	25^{l}	13.1^{op}
27 *Erucaria hispanica*	$0.576^{bcdefghi}$	19.4^{efghi}	$37.9^{ijklmnopq}$	31^{hij}	36.0^{defghi}
28 *E. ollivieri*	$0.552^{cdefghij}$	17.8^{ghijk}	50.3^{bcdefg}	38^{efghij}	23.8^{jklmno}
29 *Erucastrum varium*	$0.379^{hijklmn}$	18.5^{fghij}	47.7^{defghi}	39^{efghij}	20.9^{klmnop}
30 *E. cardaminoides*	0.706^{bc}	14.7^{nop}	$35.8^{klmnopq}$	32^{hij}	26.8^{hijklm}
31 *E. abyssinicum*	0.207^{n}	20.0^{efgh}	49.4^{cdefgh}	50^{abcdef}	11.9^{p}
32 *E. laevigatum*	$0.541^{cdefghijk}$	19.7^{efghi}	$35.8^{klmnopq}$	58^{abc}	19.8^{klmnop}
33 *E. gallicum*	0.251^{mn}	17.1^{ijklm}	50.9^{bcdef}	43^{defghi}	30.5^{fghijk}
34 *Enarthrocarpus lyratus*	$0.487^{defghijk}$	19.3^{efghi}	$44.0^{efghijklmn}$	28^{ij}	37.2^{defgh}
35 *Moricandia arvensis*	$0.522^{cdefghijk}$	14.8^{mnop}	34.4^{nopq}	$40^{defghij}$	26.2^{ijklm}
36 *Sinapis pubescens*	$0.484^{defghijk}$	20.2^{defg}	51.6^{bcde}	49^{bcdefg}	50.2^{abc}
37 *S. flexuosa*	0.663^{bcd}	12.3^{q}	$42.3^{efghijklmn}$	41^{defghi}	21.6^{klmnop}
38 *S. arvensis*	0.900^{a}	13.8^{pq}	$39.6^{hijklmnop}$	34^{ghij}	42.5^{cde}
39 *Trachystoma balli*	0.638^{bcde}	23.6^{bc}	$43.7^{efghijklmn}$	$42^{defghij}$	26.1^{ijklm}
LSD ($p = 0.05$)	0.162	2.07	8.30	12.7	9.14

the differences in SLM, but depend largely on species. Intergeneric variations in SLM at a chosen ontogenic stage can show stability of ranking from season to season (Lugg and Sinclair 1981) that is heritable (Song and Watson 1975). The positive relationship between SLM and P_N justifies the use of SLM in breeding programmes to select for high photosynthetic efficiency.

The highest seasonal mean leaf area (A) recorded was in *B. barrelieri*, while in *B. spinescens* it was the lowest. The difference between the largest and the smallest area was sevenfold. Among the cultivated species, *B. juncea* and *B. napus* produced considerably larger leaves. The leaves of C_3-C_4 intermediary, *Moricandia arvensis,* were medium sized (Table 1). A tendency for negative relationship between A and P_N was observed though not significant (Table 2, Fig. 1). The causes of the negative relationship between A and P_N are not known. It is assumed that the "dilution" hypothesis of Hesketh *et al.* (1981) may be involved since a negative relationship, though not significant, was found between A and SLM. It is also possible that the tendency for negative correlation between A and P_N has resulted from the negative association between A and SLM (Table 2, Fig. 1). An inverse relationship between A and P_N observed among wheat species and within *Triticales* (Evans and Dunstone 1970, Planchon 1979), and soybean (Barnes *et al.* 1969) is also partly a reflection of the inverse association between leaf thickness (SLM) and A. Since both A and P_N play a crucial role in determining productivity, the benefits of such a source, possessing higher P_N without significant reduction in A, in crop improvement breeding programme would be enormous.

Table 2. Correlation matrix for net photosynthetic rate (P_N), chlorophyll content (Chl), stomatal resistance (r_s), specific leaf mass (SLM) and leaf size (A) in *Brassica* coenospecies. *, ** Significant at the 0.05 or 0.01 probability level, respectively.

	Chl	r_s	SLM	A
1. P_N	0.407**	-0.341*	0.399*	-0.052
2. Chl	-	-0.249	0.585**	0.237
3. r_s		-	-0.202	0.258
4. SLM			-	-0.108

Among the *Brassica* coenospecies, mean r_s ranged from 0.21 in *Diplotaxis berthautii* to 0.76 s cm^{-1} in *B. juncea* with a 3.6 fold difference between the highest and the lowest resistances (Table 1). Cultivated species exhibited higher r_s compared to the rest. Correlations between P_N and r_s showed a significant negative relationship (Table 2, Fig. 1). This observation is similar to that reported in the cultivated species of *Brassica* by Hobbs (1988). The Chl content varied from 22.0 in *B. juncea* to 631 mg m^{-2} in *Diplotaxis catholica* (Table 1). Positive relationship between P_N and Chl content observed in this study is in accordance with that of Hobbs (1988). The positive bearing of Chl content on P_N can be viewed in terms of its role in radiant energy absorption and transfer. In the present investigation, species × date of measurements interactions were significant only for P_N in 1993, and for Chl content in 1994. Both cases were, however, very small compared to the species variability.

Species × year interactions were significant only for r_s.

The results of the present survey consisting of 39 *Brassica* coenospecies suggest that large genetic potential exists for the improvement of P_N and other leaf characters.

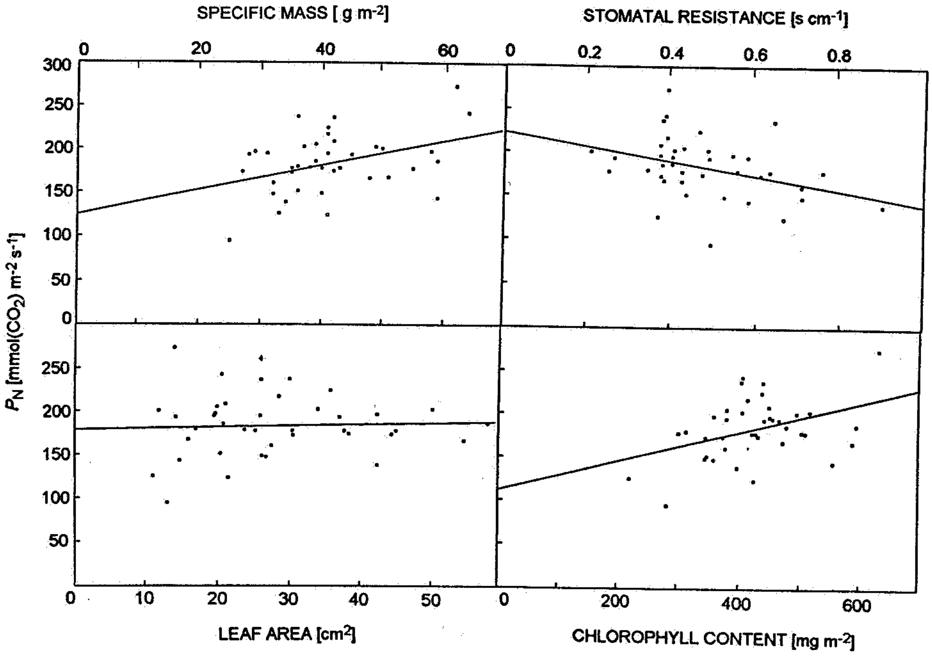

Fig. 1. Relationship between net photosynthetic rate (P_N) and related parameters in *Brassicaceae* coenospecies.

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