Theor Appl Genet (1991) 81:64–70

THEORETICAL AND APPLIED GENETICS

Leaf physiological aspects of nitrogen-use efficiency in *Brassica campestris* L.: quantitative genetic variation across nutrient treatments

A. S. Evans *

Department of Ecology and Evolution, The University of Chicago, Chicago, IL 60637, USA

Received October 10, 1989; Accepted April 23, 1990
Communicated by A. R. Hallauer

Summary. Quantitative genetic parameters for leaf physiological and whole-plant aspects of nitrogen-use efficiency in *Brassica camprestris* L. were estimated in three nutrient treatments in the greenhouse. Narrow-sense heritabilities and genetic correlations varied across treatments for some traits. Sire effects were significant for leaf nitrogen content in near-optimal and super-optimal, but not in suboptimal nutrient treatments. Additive genetic variation for two estimates of leaf physiological nitrogen-use efficiency (nitrogen-based photosynthetic capacity and leaf carbon : nitrogen ratio) was significant only in the suboptimal nutrient treatment. Area-based photosynthetic capacity, on the other hand, exhibited no heritable variation in any nutrient treatment. Heritability estimates of aboveground biomass and flower production were greatest in sub- and super-optimal treatments, respectively. Negative genetic correlations between leaf nitrogen content and both estimates of leaf nitrogen-use efficiency were evident in the super-optimal treatment. Aboveground biomass and leaf nitrogen-use efficiency were positively correlated in the suboptimal treatment, suggesting that growth differences were due in part to the efficiency with which nitrogen was utilized in physiological processes. Although implications for breeding may differ for different sources of germ plasm or different measures of performance or yield, selection for improved whole-plant performance through increased nitrogen-use efficiency should proceed best in suboptimal nutrient treatments.

Key words: Photosynthesis – Aboveground biomass – Heritability – Genetic correlation – Rapid cycling base population

Introduction

Understanding selection of wild species or breeding potential of crop species both require knowledge of the genetic bases of physiological processes in plants. Some physiological traits may be more important than others. For example, photosynthesis is basic to plant growth and reproduction, but instantaneous measurements of photosynthetic capacity are generally not good predictors of crop yield (Elmore 1980; Evans 1975; Lambers 1987; Lechowicz 1984; Zelitch 1982). The efficiency with which physiological processes, such as photosynthesis, proceed may be more predictive of yield than the rate per se. While efficiency can be explored with respect to any limiting resource, problems with nitrogen fertilization (cost, availability, and environmental impact) of crop species have led to increased research on the efficiency with which applied nitrogen is utilized. Genetic variation for yield components in different fertilizer regimes has been identified for several crop species, e.g., corn, *Zea mays* L. (Moll et al. 1982), rice, *Oryza sativa* L. (Broadbent et al. 1987), winter wheat, *Triticum aestivum* L. (Van Sanford and MacKown 1986), millet, *Pennisetum glaucum* (L.) R. Br. (Alagarswamy et al. 1988), and spring rape, *Brassica napus* L. (Yau and Thurling 1987a, b). However, these studies have not examined leaf physiological aspects of phenotypic or genetic differences in whole-plant nitrogen-use efficiency (but see Alagarswamy et al. 1988).

Previous work (Evans 1989) with *B. campestris* L. (syn. *rapa*) documented phenotypic variation across three nutrient treatments (suboptimal, near-optimal, and super-optimal) in some leaf physiological traits that are important in whole-plant nitrogen-use efficiency. Instantaneous estimates of area-based photosynthetic capacity were not significantly correlated with either total above-

---

* Present address: Department of Biology, Unversity of New Mexico, Albuquerque, NM 87131, USA

ground biomass or flower production in any treatment. In the super-optimal treatment, leaf nitrogen content (per unit area) was negatively correlated with flower production. Nitrogen-based photosynthetic capacity (an instantaneous estimate of the efficiency with which nitrogen is utilized in photosynthesis) showed a low but significant positive correlation with flower production in near- and super-optimal, but not suboptimal treatments. The ratio of leaf carbon to nitrogen contents (a long-term estimate of leaf nitrogen-use efficiency that is integrated over the lifetime of the tissue) was positively correlated with both aboveground biomass and flower production in all three treatments.

Just as phenotypic correlations change across treatments, so may genetic parameters which influence the potential for response to selection for useful leaf physiological traits. Hence, regardless of the environment in which crops are ultimately to be grown, some environments (which maximize the expression of heritable variation) may be more useful than others for improving yield by artificial selection for desirable traits (Falconer 1952). My objective was to estimate quantitative genetic parameters for leaf physiological traits in *B. campestris*. Heritabilities were calculated for leaf physiological and whole-plant performance traits using families grown in three nutrient treatments in the greenhouse. Genetic correlations between and among leaf physiological and whole-plant performance traits were calculated for each treatment.

Materials and methods

Plant material

The genus *Brassica* (Cruciferae) contains several agriculturally important vegetable, oil, and fodder species. To facilitate research on diverse aspects of *Brassica* biology, rapid-cycling base populations (RCBPs) of economically important *Brassica* species were developed through 10% artificial selection for reduced reproductive time on large populations (≥ 288 plants) of diverse, early flowering types (Williams and Hill 1986). Phenotypically, RCBPs respond strongly to various environmental variables and show considerable isozyme variation (Williams and Hill 1986). Seeds of RCBP *Brassicas* may be obtained from the Crucifer Genetics Cooperative (Department of Plant Pathology, University of Wisconsin-Madison). These stocks can be used to identify potentially useful traits that can be explored in or transferred to commercially important *Brassica* populations.

RCBP *B. campestris* (CrGC-1, $n = 10$) is characterized by rapid onset of flowering (as few as 14 days from planting), rapid seed maturation (20–30 days from pollination), absence of seed dormancy, high female fertility, and petite habit (Williams and Hill 1986). The obligately outcrossing flowers are hermaphroditic with a sporophytic self-incompatibility system. Significant levels of inbreeding depression suggest that the base population did not undergo a genetic bottleneck during artificial selection (A. S. Evans, unpublished results).

Experimental design

Seeds of RCBP *B. campestris* were planted in commercial potting medium (Pro-Mix) and used as parents in a replicated complete factorial breeding design which permitted assessment of sire × dam interactions and maternal effects. Eight parents were used as pollen donors (sires) and the remaining 12 were used as seed parents (dams). Groups of two sires and three dams were completely crossed to produce six full-sib families: three half-sib families for each sire and two half-sib families for each dam. Four such groups were used to produce a total of 24 full-sib families. Ten or fewer (mean = 9.95) progeny of each family were planted in commercial potting mix (Pro-Mix) and grown in each of three nutrient treatments in The University of Chicago greenhouse. The treatments were effected with fertilizer applications corresponding to 0, 100, and 200 ppm added N (Peters 20% N, 19% P, 18% K, and essential micronutrients). Treatments were begun at planting and were applied with every ad libitum watering to maintain each nutrient regime throughout the experiment. The treatments were selected on the basis of a pilot experiment to correspond to suboptimal, near-optimal, and super-optimal growth conditions and are referred to as LOW, MEDIUM, and HIGH, respectively. Both aboveground biomass accumulation and flower production were lowest in LOW (0.07 g-dry and 7, respectively). Although aboveground biomass accumulation was not significantly different in MEDIUM (0.56 g-dry) and HIGH (0.52 g-dry), flower production was depressed in HIGH (20) relative to MEDIUM (34) (Evans 1989).

Measured and derived traits

Plant traits were measured 30–35 days after planting when most individuals had commenced flowering but were not senescent. Leaf physiological traits were measured as follows. Area-based photosynthetic capacity was estimated from CO_2 uptake at saturating PAR (2300 μmol $m^{-2}\ s^{-1}$) and ambient temperature (17°–27 °C) with a Model LCA-2 infrared gas analyzer (Analytical Development Co., Ltd.). The most recent fully expanded leaf (usually the third or fourth) of each plant was excised and immediately placed in a Parkinson cuvette. All photosynthetic rates were measured between 800 and 1,200 h over the course of 4 days. Discs of known area were removed from the leaves used to measure photosynthesis, freeze-dried, weighed to determine specific leaf weight (mass per area), and then used for elemental analyses. Percentages of leaf tissue composed of carbon and nitrogen were measured with a Perkin-Elmer Model 2400 CHN elemental analyzer and used to calculate area-based carbon and nitrogen contents. I calculated two estimates of leaf physiological nitrogen-use efficiency, carbon : nitrogen ratio (long-term nitrogen-use efficiency) and nitrogen-based photosynthetic capacity (instantaneous nitrogen-use efficiency). Two components of whole-plant performance were measured on individual plants: number of flowers produced and total aboveground biomass (dry weight basis).

Statistical analyses

All statistical analyses were performed using procedures of SAS Institute, Inc. (1985). Analyses of photosynthesis data were based on residuals from an ANOVA designed to remove the effects of day and time of measurement (Evans 1989). The method of Wright (1968) was used to transform all variables to meet the ANOVA assumption of homoscedasticity.

Both sire- and dam-based heritabilities were calculated for each trait in each treatment when indicated by a significant ANOVA. A type II ANOVA using type III sums of squares was based on the model:

$$X_{ijk} = u + s_i + d_j + (s \times d)_{ij} + e_{ijk} \ ,$$

where X_{ijk} represents the value of the dependent variable in the k^{th} progeny of the i^{th} sire and the j^{th} dam, s_i and d_j represent the effects of sire i and dam j, respectively, $(s \times d)_{ij}$ represents the interaction between sire and dam, and e_{ijk} represents the error variance. If the sire × dam effect was nonsignificant, a second ANOVA was performed based on a model that omitted the sire × dam effect. Components of variance were calculated using SAS-generated equations for the expected mean squares. Sire- and dam-based heritabilities were calculated from genetic models (Falconer 1981):

$$\sigma^2_{\text{sire}} = \text{cov}_{\text{half-sib (sire)}} = (1/4)\,V_A\ ,$$
$$h^2_{\text{sire}} = 4\sigma^2_{\text{sire}}/\sigma^2_{\text{total}}\ ;$$
$$\sigma^2_{\text{dam}} = \text{cov}_{\text{half-sib (dam)}} = (1/4)\,V_A + M\ ,$$
$$h^2_{\text{dam}} = 4\sigma^2{}_{\text{dam}}/\sigma^2_{\text{total}}\ ,$$

in which all sources of epistatic variation were assumed to be negligible. In this design, dam-based heritabilities include maternal environmental and nonnuclear genetic variation as well as additive genetic variation. A larger dam heritability than sire heritability suggests that maternal effects were important. Standard errors of heritabilities were estimated according to Falconer (1981).

Genetic correlations among traits were estimated from full-sib family means. This technique approximates genetic correlations based on genetic components and includes some within-family error variance (Via 1984). As family size increases, family mean correlation should approach the true genetic correlation. Significance testing is possible for the family mean technique but not the genetic component procedure. Correction of significance levels for multiple comparisons is advisable for large tables of correlation coefficients (Miller 1981). For this reason, in addition to individual significance levels, I calculated significance levels adjusted (for each grouping of traits within treatments) for the number of simultaneous comparisons, using the sequential Bonferroni procedure of Rice (1989). To test whether genetic correlations differed among nutrient treatments, I used a Chi-square test of z-transformed data (Steel and Torrie 1960).

Results and discussion

Heritabilities

Due to sample size, which was limited by the costs of measuring physiological traits, the existence of significant heritable variation was conservatively estimated. Additive genetic variation, estimated by sire-based heritabilities, varied across treatments for some traits (Table 1).

Sire effects were not significant for area-based photosynthetic capacity in any nutrient treatment. This result may be a function of the small sample size. However, Paul and Eagles (1988) suggested that there may be a limited range of variability for this trait in *Brassica* species. They found significant variation for area-based photosynthetic rate among cultivars of *B. oleracea* L., but not among cultivars of *B. campestris* or *B. napus*.

In the same study, cultivar differences in leaf area per mass (the inverse of specific leaf weight) were found for *B. oleracea* and *B. napus* but not for *B. campestris*. In the present study, there was no significant sire-based heritable variation for specific leaf weight in the near-optimal (MEDIUM) treatment, most similar to that used by Paul and Eagles (1988). However, in the nutrient-limited treatment (LOW) there was significant variation among sires in specific leaf weight. Similar results were found for leaf carbon content. The high phenotypic ($r \geq 0.95$; $p < 0.0001$) and genetic (Table 2) correlations between specific leaf weight and leaf carbon content in all three treatments suggest that these two traits measure the same leaf physiological trait.

For leaf nitrogen content, sire-based heritabilities were significant in MEDIUM and HIGH but not LOW. Yau and Thurling (1987 a) found a similar result for nitrogen uptake per unit root biomass in *B. napus*: differences among 40 cultivars were significant only in intermediate levels of nitrogen supply. They suggested that genetic differences in nitrogen uptake capability cannot be expressed in conditions of severely limited nitrogen supply since available nitrogen is quickly exhausted. Moreover,

Table 1. Additive genetic and maternal variation of traits in three nutrient treatments. Significant heritabilities based on sire (h^2_s) and dam (h^2_d) half-sib families are followed by standard errors

Trait[a]	Nutrient environment					
	LOW		MEDIUM		HIGH	
	h^2_s	h^2_d	h^2_s	h^2_d	h^2_s	h^2_d
Area-based photosynthetic capacity	NS	NS	NS	NS	NS	NS
Specific leaf weight	0.56 (0.08)	0.11 (0.01)	NS	NS	NS	0.52 (0.07)
Leaf carbon content	0.57 (0.08)	0.48 (0.07)	NS	NS	NS	0.48 (0.07)
Leaf nitrogen content	NS	NS	0.31 (0.04)	NS	0.21 (0.03)	0.35 (0.05)
Nitrogen-based photosynthetic capacity	0.26 (0.04)	NS	NS	NS	NS	NS
Leaf carbon : nitrogen	1.22[b] (0.18)	0.27 (0.04)	NS	NS	NS	NS
Aboveground biomass	0.97[b] (0.18)	0.59 (0.08)	NS	NS	0.26 (0.03)	NS
Flower production	NS	0.23 (0.03)	NS	0.31 (0.04)	0.92 (0.12)	NS

[a] Units:
Area-based photosynthetic capacity, μmol CO_2 m^{-2} s^{-1}
Specific leaf weight, g m^{-2}
Leaf carbon content, mol C m^{-2}
Leaf nitrogen content, mol N m^{-2}
Nitrogen-based photosynthetic capacity
(instantaneous nitrogen-use efficiency), μmol CO_2 mol N^{-1} s^{-1}
Leaf carbon : nitrogen content
(long-term nitrogen-use efficiency), ratio
Aboveground biomass, g-dry
Flower production, number

[b] Estimates for which the sire × dam interaction term was significant

Table 2. Genetic correlations among physiological traits in three nutrient treatments

Traits[a]	Nutrient environment		
	LOW	MEDIUM	HIGH
Area-based photosynthetic capacity	0.53[b]	0.40	0.28
Specific leaf weight	(0.0076)	(0.0540)	(0.1922)
Area-based photosynthetic capacity	0.56	0.44	0.27
Leaf carbon content	(0.0048)*	(0.0300)	(0.2040)
Area-based photosynthetic capacity	0.65	0.49	0.12
Leaf nitrogen content	(0.0006)**	(0.0144)	(0.5763)
Area-based photosynthetic capacity	0.09	0.07	0.16
Leaf carbon : nitrogen	(0.6701)	(0.7404)	(0.4655)
Area-based photosynthetic capacity	0.35	0.48	0.46
Nitrogen-based photosynthetic capacity	(0.0905)	(0.0155)	(0.0231)
Nitrogen-based photosynthetic capacity[c]	0.11	−0.39	−0.56
Specific leaf weight	(0.5969)	(0.0601)	(0.0047)*
Nitrogen-based photosynthetic capacity[c]	0.11	−0.37	−0.59
Leaf carbon content	(0.5940)	(0.0704)	(0.0025)*
Nitrogen-based photosynthetic capacity	−0.35	−0.51	−0.79
Leaf nitrogen content	(0.0903)	(0.0115)	(0.0001)**
Nitrogen-based photosynthetic capacity[c]	0.45	0.14	0.73
Leaf carbon : nitrogen	(0.0261)	(0.5072)	(0.0001)**
Specific leaf weight	0.98	0.97	0.99
Leaf carbon content	(0.0001)**	(0.0001)**	(0.0001)**
Specific leaf weight[c]	0.47	0.79	0.86
Leaf nitrogen content	(0.0194)	(0.0001)**	(0.0001)**
Specific leaf weight[c]	0.71	0.48	−0.28
Leaf carbon : nitrogen	(0.0001)**	(0.0189)	(0.1748)
Leaf carbon content[c]	0.49	0.83	−0.29
Leaf nitrogen content	(0.0153)	(0.0001)**	(0.1748)
Leaf carbon content[c]	0.70	0.50	−0.30
Leaf carbon : nitrogen	(0.0001)**	(0.0120)	(0.1580)
Leaf nitrogen content[c]	−0.27	−0.06	−0.72
Leaf carbon : nitrogen	(0.2100)	(0.7685)	(0.0001)**

[a] Units as in Table 1

[b] Pearson's correlation coefficients are followed by individual significance levels (uncorrected for simultaneous comparisons). Symbols indicate significance levels after Bonferroni correction for simultaneous comparisons (* $p<0.05$; ** $p<0.01$)

[c] Pairs of traits for which correlation coefficients varied significantly across treatments

they reported low heritabilities (≤ 0.1) for F_2 progeny from a cross of 2 of the 40 cultivars when nutrients were abundant in both field and phytotron experiments (Yau and Thurling 1987b). These results are, however, not directly comparable to the present work, since leaf nitrogen content can be influenced by nitrogen partitioning among plant organs and total root biomass as well as by nitrogen uptake per unit root biomass.

The two estimates of leaf nitrogen-use efficiency, nitrogen-based photosynthetic capacity (instantaneous nitrogen-use efficiency) and leaf carbon : nitrogen ratio (long-term leaf nitrogen-use efficiency), exhibited significant sire-based heritable variation only in the suboptimal LOW treatment. These results were not unexpected since potential differences in nitrogen utilization should be most evident when nitrogen is limiting growth. Although leaf physiological components of nitrogen-use efficiency are not directly comparable to yield-based measurements of nitrogen-use efficiency (biomass per unit nitrogen absorbed), Yau and Thurling (1987a) reported differences among *B. napus* cultivars in yield-based nitrogen-use efficiency only in low-nitrogen treatments. A similar result was reported for tomato, *Lycopersicon esculantum* Mill. (O'Sullivan et al. 1974). Alagarswamy et al. (1988) reported differences for nitrogen-based photosynthetic capacity among four pearl millet genotypes grown in four nutrient treatments. However, environmental dependence of genetic differences was not explored since the data were pooled over treatments.

For total aboveground biomass, sire-based heritable variation was significant in LOW and HIGH, but not MEDIUM. Flower production showed a significant effect of sire only in HIGH, likely because of flower bud abortion in that treatment (personal observation). Yau and Thurling (1987a) also reported environmental dependence of cultivar differences for several components of yield (seed yield, growth rate, dry weight, and harvest index) in *B. napus*.

In two instances (leaf carbon : nitrogen ratio and total aboveground biomass in LOW), interpretation of sire- and dam-based heritabilities should be viewed with caution since sire × dam interactions were significant. Maternal effects (based on larger dam- than sire-based heritability) appeared to be important for specific leaf weight and leaf carbon content in HIGH, as well as for flower production in LOW and MEDIUM. Nonadditive effects were reported for components of yield in *B. campestris* (Sharma 1978) and *B. napus* (Duhoon et al. 1982).

Significant sire effects were found in the absence of significant dam effects in several instances (e.g., flower production in HIGH). In the breeding design used, dams and sires formed mutually exclusive groups. Therefore, traits that show a significant dam effect should not necessarily be expected to show a significant sire effect. This result suggests that the heritability estimates presented here were influenced by the particular set of parents used. Since parents were randomly drawn from the base population and randomly mated, a larger sample of parents is needed to avoid anomalous results.

Genetic correlations

For some pairs of traits, genetic correlation coefficients differed among nutrient treatments (Tables 2 and 3). If each correlation is considered in isolation, coefficients above approximately 0.4 were significant at $p \leq 0.05$. However, with the small sample size (24 full-sib families) used in this work, only coefficients above approximately 0.6 were significant after application of the sequential Bonferroni correction of Rice (1989). Consequently, the results are interpreted conservatively.

Among some physiological traits, differences in genetic correlations across environments were evident (Table 2). Leaf carbon content and leaf nitrogen content were positively correlated with area-based photosynthetic capacity in LOW and were negatively correlated with nitrogen-based photosynthetic capacity in HIGH. Specific leaf weight was positively correlated with leaf nitrogen in MEDIUM and HIGH and with leaf carbon : nitrogen ratio in LOW. Specific leaf weight and leaf carbon content, as noted earlier, were strongly positively correlated in all three treatments.

The two leaf physiological components of nitrogen-use efficiency (nitrogen-based photosynthetic capacity and leaf carbon : nitrogen ratio) were positively correlated in HIGH. The same trend was significant, when considered in isolation, in LOW. However, both estimates of nitrogen-use efficiency were negatively correlated with leaf nitrogen content in HIGH. Van Sanford and MacKown (1986) reported no significant genetic correlation between flag-leaf nitrogen concentration and yield-based nitrogen-use efficiency in wheat. In *B. napus*, the efficiencies of nitrogen uptake and utilization were not genetically correlated (Yau and Thurling 1987b).

The two estimates of whole-plant performance, aboveground biomass and flower production, showed a positive genetic correlation in LOW and MEDIUM but not in HIGH (Table 3).

Few genetic correlations between leaf physiological and whole-plant performance traits were significant after application of the Bonferroni correction for simultaneous comparisons (Table 3). In LOW, both the instantaneous (nitrogen-based photosynthetic capacity) and the long-term (carbon : nitrogen ratio) estimates of leaf nitrogen-use efficiency were positively correlated with aboveground biomass. Genetic correlations of these two traits with flower production were significant in LOW and HIGH before correction for simultaneous comparisons. Similar stress-dependent results were reported for *B. napus*: there was a positive genetic correlation between yield-based nitrogen-use efficiency and some components of yield when nutrients were limiting (Yau and Thurling 1987a), but not when nutrients were abundant (Yau and Thurling 1987b). Among pearl millet genotypes, however, differences in nitrogen-based photosynthesis were not large enough to explain differences in yield-based nitrogen-use efficiency (Alagarswamy et al. 1988).

Table 3. Genetic correlations among physiological and whole-plant performance traits in three nutrient treatments

Traits[a]	Nutrient environment		
	LOW	MEDIUM	HIGH
Aboveground biomass[c] Flower production	0.64[b] (0.0007)**	0.69 (0.0002)**	0.11 (0.5975)
Aboveground biomass Area-based photosynthetic capacity	0.01 (0.9636)	−0.02 (0.9316)	−0.45 (0.0268)
Flower production Area-based photosynthetic capacity	−0.29 (0.1715)	−0.37 (0.0782)	−0.07 (0.7292)
Aboveground biomass[c] Nitrogen-based photosynthetic capacity	0.57 (0.0036)*	0.31 (0.1386)	−0.27 (0.1961)
Flower production Nitrogen-based photosynthetic capacity	0.47 (0.0219)	0.18 (0.4026)	0.46 (0.0234)
Aboveground biomass Specific leaf weight	0.40 (0.0501)	−0.12 (0.5799)	−0.09 (0.6926)
Flower production Specific leaf weight	−0.01 (0.9303)	−0.44 (0.0334)	−0.40 (0.0509)
Aboveground biomass Leaf carbon content	0.37 (0.0792)	−0.14 (0.5201)	−0.07 (0.7448)
Flower production Leaf carbon content	−0.01 (0.9533)	−0.50 (0.0134)	−0.42 (0.0390)
Aboveground biomass Leaf nitrogen content	−0.39 (0.0606)	−0.29 (0.1736)	0.04 (0.8633)
Flower production Leaf nitrogen content	−0.49 (0.0163)	−0.50 (0.0129)	−0.53 (0.0083)
Aboveground biomass[c] Leaf carbon : nitrogen	0.77 (0.0001)**	0.19 (0.3760)	−0.27 (0.1961)
Flower production Leaf carbon : nitrogen	0.45 (0.0291)	−0.12 (0.5628)	0.45 (0.0286)

[a] Units as in Table 1

[b] Pearson's correlation coefficients are followed by individual significance levels (uncorrected for simultaneous comparisons). Symbols indicate significance levels after Bonferroni correction for simultaneous comparisons (* $p < 0.05$; ** $p < 0.01$)

[c] Pairs of traits for which correlation coefficients varied significantly across treatments

Implications for breeding

Genetic differences in performance at equivalent nutrient supply indicate genetic differences in nutrient uptake and/or utilization efficiency. The positive genetic correlations between whole-plant performance and leaf physiological aspects of nitrogen-use efficiency in LOW suggest that performance differences were due in part to the efficiency with which nitrogen was utilized in photosynthesis. Since aboveground biomass as well as instantaneous and long-term estimates of leaf physiological nitrogen-use efficiency exhibited additive genetic variation in LOW, nitrogen-limiting growth conditions could be used to attain improvements in biomass. Furthermore, selection on one leaf physiological component of nitrogen-use efficiency should provide a positive correlated response in the other. In this regard, carbon : nitrogen ratio may be easier, although more expensive, to measure than nitrogen-based photosynthetic capacity.

Several authors (Yau and Thurling 1987a, b; Van Sanford and MacKown 1986) have suggested that nitrogen uptake may be a useful trait for improvement of yield-based nitrogen-use efficiency. However, Moll et al. (1982) pointed out that causes of efficient nitrogen use may differ among nutrient environments and genotypes. In the present work, nitrogen uptake was not directly measured, but there was additive genetic variation for leaf nitrogen content in HIGH and MEDIUM. However, selection for nitrogen uptake or content when nitrogen is abundant might be counterproductive for two reasons. First, there was a negative genetic correlation between leaf nitrogen content and both leaf physiological components of nitrogen-use efficiency in HIGH, which suggests that increased uptake and use efficiency could not be simultaneously attained in RCBP *B. campestris*. Second, there was a marginally significant negative genetic correlation between leaf nitrogen content and flower production in all nutrient treatments, which suggests disadvantageous nitrogen allocation properties in this population.

Together these results indicate that in RCBP *B. campestris*, selection for improved performance through improved leaf nitrogen-use efficiency should proceed best in conditions of limiting nutrient supply. Although implications for breeding may be different for different sources of germ plasm or different measures of performance or yield, the genetics of physiological efficiency warrant further study in both wild and crop species.

Acknowledgements. Thanks to P. Williams of the Crucifer Genetics Cooperative for information about the development and attributes of rapid-cycling *Brassicas* and to the greenhouse staff of The University of Chicago, E. McCarthy, W. Schroeder, and S. Yamins, for their assistance in caring for the plants. Aid in planting and/or sampling was generously provided by J. Brown, M. Johnston, A. Peterson, T. Peterson, W. Pope, J. Teeri, J. Vitale, and A. Winn. The carbon and nitrogen assays were made possible by J. Teeri and were conducted by S. Hendricks. A. Hallauer, D. Marshall, T. Nusbaum, D. Schemske, J. Teeri, M. Wade, C. Wisdom, and an anonymous reviewer made helpful suggestions on the manuscript. This research was supported by the Hinds Fund of The University of Chicago, NIH-GM07197 Training Grant in Genetics to The University of Chicago, and NSF-BSR-8705888 to J. Teeri of the University of Michigan.

References

Alagarswamy G, Gardner JC, Maranville JW, Clark RB (1988) Measurement of instantaneous nitrogen use efficiency among pearl millet genotypes. Crop Sci 28:681–685

Broadbent FE, DeDatta SK, Laureles EV (1987) Measurement of nitrogen utilization efficiency in rice genotypes. Agron J 79:786–791

Duhoon SS, Chandra S, Basu AK, Makhija OP (1982) Components of genetic variation for yield and its attributes in a diallel cross of yellow-seeded Indian colza *Brassica napus* var. *glauca*. Indian J Agric Sci 52:154–158

Elmore CD (1980) The paradox of no correlation between leaf photosynthetic rates and crop yields. In: Hesketh JD, Jones JW (eds) Predicting photosynthesis for ecosystem models. CRC Press, Boca Raton, pp 155–164

Evans AS (1989) Phenotypic plasticity of physiological and life history characteristics: evolutionary implications in rapid-cycling *Brassica campestris* L. PhD Thesis, The University of Chicago

Evans LT (1975) The physiological basis of crop yield. In: Evans LT (ed) Crop physiology: some case histories. Cambridge University Press, Cambridge, pp 327–355

Falconer DS (1952) The problem of environment and selection. Am Nat 86:293–298

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, New York

Lambers H (1987) Does variation in photosynthetic rate explain variation in growth rate and yield? Neth J Agric Sci 35:505–519

Lechowicz MJ (1984) The effects of individual variation in physiological and morphological traits on the reproductive capacity of the common cocklebur, *Xanthium strumarium* L. Evolution 38:833–844

Miller RG Jr (1981) Simultaneous statistical inference. McGraw Hill, New York Toronto London

Moll RH, Kamprath EJ, Jackson WA (1982) Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agron J 74:562–564

O'Sullivan J, Gabelman WH, Gerloff GC (1974) Variation in efficiency of nitrogen utilization in tomatoes (*Lycopersicon esculentum* Mill.) grown under nitrogen stress. Am Soc Hortic Sci 99:543–547

Paul NK, Eagles CF (1988) Cultivar differences in net photosynthetic rate and their relationship with anatomical characteristics in *Brassica*. Photosynthetica 22:320–327

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

SAS Institute, Inc. (1985) SAS user's guide: statistics, version 5 edn. SAS Institute, Inc., Carey/NC

Sharma JR (1978) Components of genetic variation for some yield attributes in relation to self-incompatibility in *Brassica campestris* var. Brown. Crop Improv 5:29–36

Steel RGD, Torrie JH (1960) Principles and procedures of statistics. McGraw-Hill, New York Toronto London

Van Sanford DA, MacKown CT (1986) Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theor Appl Genet 72:158–163

Via S (1984) The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. Evolution 38:896–905

Williams PH, Hill CB (1986) Rapid-cycling populations of *Brassica.* Science 232:1385–1389

Wright S (1968) Evolution and the genetics of populations, vol I, genetics and biometric foundations. The University of Chicago Press, Chicago

Yau SK, Thurling N (1987a) Variation in nitrogen response among spring rape (*Brassica napus*) cultivars and its relationship to nitrogen uptake and utilization. Field Crop Res 16:139–155

Yau SK, Thurling N (1987b) Genetic variation in nitrogen uptake and utilization in spring rape (*Brassica napus* L.) and its exploitation through selection. Plant Breed 98:330–338

Zelitch I (1982) The close relationship between net photosynthesis and crop yield. BioScience 32:796–802