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Constraint to Adaptive Evolution in Response to Global Warming

Julie R. Etterson*† and Ruth G. Shaw

We characterized the genetic architecture of three populations of a native North American prairie plant in field conditions that simulate the warmer and more arid climates predicted by global climate models. Despite genetic variance for traits under selection, among-trait genetic correlations that are antagonistic to the direction of selection limit adaptive evolution within these populations. Predicted rates of evolutionary response are much slower than the predicted rate of climate change.

Plants have responded to historical climate change by migration and adaptation (*1*). However, habitat fragmentation is likely to impede migration in the future (*2*). Furthermore, migration may be slower than during the recession of the glaciers, because migration will depend on seedling establishment in occupied habitats (*3*). The persistance of populations thus hindered from spread into higher latitudes may depend more heavily on adaptive evolution.

Evolutionary response requires genetically based variation among individuals. However, even given this substrate for natural selection, evolution may be constrained by genetic correlations among traits that are not in accord with the direction of selection (*4*, *5*), correlations termed "antagonistic." For example, if selection favors high values of two traits but these traits are negatively genetically correlated, selection response can be inhibited (Fig. 1A).

We evaluated the evolutionary potential of three populations of the native annual legume *Chamaecrista fasciculata*, which were sampled from an aridity gradient in tallgrass prairie fragments in the U.S. Great Plains (Fig. 2A) (*6*). Natural selection on phenotypic variation in *C. fasciculata* differs across this geographic range (*7*). Field and common garden studies of Minnesota (MN), Kansas (KS), and Oklahoma (OK) populations of *C. fasciculata* demonstrated clinal variation and genetic divergence with respect to physiological and morphological traits (*7*). Greenhouse drought experiments also demonstrated adaptation of these populations to different water availability conditions; northern plants are less drought-tolerant than southern plants (*7*).

We used this spatial gradient in climate as a proxy for the temporal trend in climate predicted for northern populations with global warming. For example, one global climate model predicts that the MN population will experience soil moisture conditions similar to the current climate of KS by 2025–2035 (Fig. 2B) (*8*). To predict rates of adaptation to climate change, we estimated evolutionary trajectories for three populations reciprocally planted in three environments. The evolutionary trajectory of a northern population reared in progressively more southern sites provides insight into the population's adaptive potential in the face of global warming.

We produced pedigreed seeds for MN, KS, and OK populations by controlled crosses in the greenhouse according to a standard quantitative genetic design (*9*). Progeny from these crosses were reciprocally planted into field sites in MN, KS, and OK (*10*). We measured traits subject to differing natural selection under distinct drought regimes (fecundity and leaf number) or varying clinally across the geographic range of this study (leaf thickness and the rate of phenological development) (*7*). In mid-summer we recorded the leaf number and reproductive stage of each plant (*11*) and collected the uppermost fully expanded leaf. At the natural end of the growing season, we recorded total pod number and seed counts from three representative pods; from these measures, we estimated total lifetime fecundity (*12*).

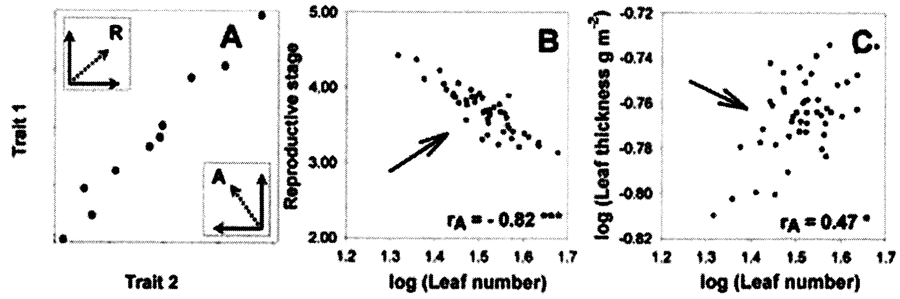

Fig. 1. Illustration of the influence of genetic correlations among traits on selection response. (**A**) Hypothetical positive genetic correlation (r_A) between two traits (each point represents the breeding value for each of two traits). There are two selection scenarios. For R (reinforcing), selection is in the same direction on traits; the depicted r_A is in accord with the direction of selection, enhancing evolutionary response; thus, the genetic correlation is reinforcing. For A (antagonistic), selection is in the opposite direction for both traits; r_A is antagonistic to the direction of selection, inhibiting evolutionary response. (**B**) Scatter plot of MN population reproductive stage and leaf number breeding values (centered on the phenotypic mean), showing signficant negative genetic correlation that is antagonstic to the positive vector of joint selection on these traits. (**C**) Scatter plot of the MN population leaf thickness and leaf number breeding values (centered on the phenotypic mean), showing signficant positive genetic correlation that is antagonistic to the negative vector of joint selection.

University of Minnesota, Department of Ecology, Evolution and Behavior, Minnesota Center for Community Genetics, 1987 Upper Buford Circle, St. Paul, MN 55108, USA.

*To whom correspondence should be addressed.
†Present address: University of Virginia, Department of Biology, Glimer Hall, Charlottesville, VA 22903, USA. E-mail: jre7e@virginia.edu

We used restricted maximum likelihood (REML) (*13*, *14*) to conduct multivariate quantitative genetic analyses of all the traits jointly to obtain estimates of the additive genetic covariance ($\mathrm{Cov}_{A_{ij}}$) between all pairs of traits for each population in each site (*15*). The predicted change in a trait ($\Delta\bar{z}$) resulting from a single generation of natural selection on phenotypic variation is simply the additive genetic covariance between relative fitness and that trait (*16*, *17*) when other traits under selection are taken into account

$$\Delta\bar{\mathbf{z}} = \mathrm{Cov}_{A}[w, \mathbf{z}] \tag{1}$$

where w is individual relative fitness (absolute fitness divided by mean fitness), and $\mathbf{z}$ is the vector of traits. Although these predictions take into account all the traits under consideration, they could be modified by selection on other genetically correlated traits that have not been considered (*18*, *19*).

These evolutionary trajectories are based on the narrow-sense heritability and the strength and direction of selection (Table 1), as well as on the influence of among-trait additive genetic covariance (Table 2). For comparison, we also present univariate predictions from analyses of the traits separately. These univariate predictions involve only the genetic variance and selection on a single trait and indicate expected evolutionary response if traits were genetically independent and, hence, would evolve independently.

Three cases are relevant to global warming (the MN population in KS and OK and the KS population in OK). Seed production was dramatically reduced in the nonnative populations as compared with the local population (for the MN population, 84% in KS and 94% in OK; for the KS population, 42% in OK) (Fig. 3A). In each of these cases, we predict adaptive evolution in response to climate warming, because the multivariate prediction is in a direction consistent with that of the univariate prediction. Overall, 14 of 18 evolutionary predictions of nonnative populations are toward the mean of the native population, which further supports the interpretation that the direction of evolutionary response is adaptive (none of the four exceptions are statistically significant). Yet with only one exception, the multivariate prediction of evolutionary response is less in absolute magnitude than the univariate prediction; in many cases, half or less. Considering the MN population grown in KS and OK, selection favoring plants bearing more and thicker leaves is expected to result in evolutionary change consistent with the direction of selection but less than if the traits evolve independently. The prediction of evolutionary response for reproductive stage of MN plants in KS (slower) is opposite that of OK (faster), which may reflect

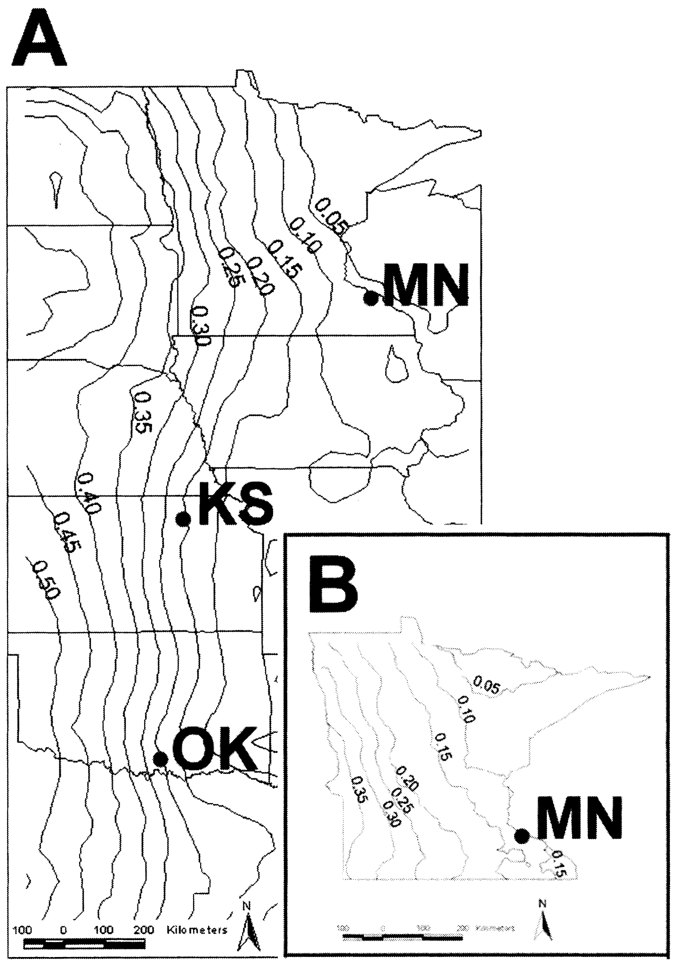

Fig. 2. (**A**) Three focal populations in Minnesota, Kansas, and Oklahoma, shown with long-term average isoclines of α for evergreen trees [1951–1980 (*25*)]. α is an integrated measure of seasonal growth-limiting drought stress on plants that accounts for temperature, precipitation, and soil texture. (**B**) Twenty-five to 35– year prediction of α for Minnesota (*8*).

Table 1. The multivariate prediction of evolutionary response after one generation of selection, $\mathrm{Cov}_A[w, \mathbf{z}]$, for three traits measured on three populations of *C. fasciculata* reared in three environments. Univariate predictions and narrow-sense heritabilities, h^2 (*6*), from separate analyses are given below evolutionary trajectories. Significance levels are not corrected for multiple testing. Of the 108 tests conducted (Tables 1 and 2), one would expect to erroneously assign significance in 5.4 cases by chance alone, assuming $\alpha_{0.05}$.

		MN population			KS population			OK population		
		Reproductive stage	Leaf number	Leaf thickness log (g m^{-2})	Reproductive stage	Leaf number	Leaf thickness log (g m^{-2})	Reproductive stage	Leaf number	Leaf thickness log (g m^{-2})
MN	Multivariate	0.0068	−0.0017	−0.0000	0.0138	−0.0167	−0.0063	0.5518***	−0.1281**	−0.0030
site	Univariate	0.0029	−0.0017	0.0006	0.0292	−0.0298	−0.0087**	0.5664****	−0.1288**	−0.0075
	h^2	0.07	0.06**	0.20**	0.00	0.09***	0.18****	0.14****	0.11****	0.08
KS	Multivariate	−0.0047	0.0055**	−0.0009	−0.0033	−0.0072*	0.6077	0.0040	0.0018	0.0006
site	Univariate	−0.0076	0.0053*	−0.0019	−0.0010	0.0054*	0.7133	0.0078	0.0018	0.0005
	h^2	0.03	0.19***	0.07***	0.00	0.12****	0.11***	0.39****	0.18**	0.05**
OK	Multivariate	0.0420	0.0184	−0.0027	0.0020	0.0077*	0.0014	−0.0082*	0.0068	−0.0013**
site	Univariate	0.1169	0.0308**	−0.0031	0.0045	0.0096*	0.0016*	−0.0084	0.0078	−0.0013**
	h^2	0.23**	0.23***	0.32****	0.00	0.24****	0.30****	0.27****	0.21**	0.09**

*$P < 0.09$. **$P < 0.05$. ***$P < 0.01$. ****$P < 0.001$.

selection for different mechanisms of drought tolerance in the intermediate site versus drought avoidance in the more southern site. For transplants of southern populations to northern sites (the KS population in MN and the OK population in KS and MN), most of the multivariate predictions of evolutionary response are also less than the univariate ones.

Why is evolutionary change predicted to be slow, given the significant heritabilities of most of the traits? Numerous additive genetic correlations are antagonistic to the direction of selection jointly on pairs of traits, as shown in Fig. 1, B and C (Table 2). Among-trait correlations that oppose the direction of selection can alter evolutionary response from expectation by (i) retarding the evolutionary response of heritable traits under selection, (ii) reversing the direction of selection response from expectation, and (iii) promoting the evolutionary response of traits not under direct selection. The first case is most evident here; the second is also illustrated by the case of the KS population at the KS site, for which the multivariate prediction of reduced leaf number conflicts with the univariate prediction for leaf number increase. These findings demonstrate that genetic relationships among traits can substantially influence evolutionary change. In each case where the univariate analysis would indicate substantial evolutionary change but the multiple trait analysis predicts a smaller change, at least one among-trait additive genetic correlation is opposite in sign to the vector of selection (antagonistic; Table 2 and Fig. 1, B and C). Although few among-trait correlations are individually significant (5 of 27), they constrain the genetic architecture of these populations and alter predicted selection response from expectation.

According to the climate model cited herein, the MN population is predicted to experience climate similar to the current climate of KS in only 25 to 35 years. Making the simplistic assumptions of constant genetic variation and selection coefficients, the number of generations required before the trait means of the MN population are expected to match those of the native KS population generally exceeds the time predicted for this climate change (reproductive stage, 21; leaf number, 42; leaf thickness, 79) (Fig. 3). The MN population is predicted to achieve the local population means in OK in fewer generations because of stronger selection and greater expression of additive genetic variance. However, these are probably underestimates of the number of generations required, because strong selection over as few as 10 generations can substantially deplete genetic variation (*20*); moreover, selection coefficients would not remain constant (*21*, *22*). Furthermore, the extreme fitness costs in terms of seed production incurred by the MN population when reared in the KS or OK climate would influence the genetic variance, inbreeding, and demography of subsequent generations and hence population persistence. Thus, even though there is significant genetic variation for all but one of these traits, the rate of multivariate evolution is expected to be slower than the rate of climate change.

When the MN population is reared in the warmer and drier climates of KS and OK, slow evolutionary response is predicted even though this population harbors significant additive genetic variance for vegetative and phenological traits under selection. Similarly, little evolutionary response is predicted for the KS population at the OK site. We do not rule out the possibility that predicted selection responses that are in the direction of the local population mean but not statistically significant will, nevertheless, be biologically significant as populations experience an incrementally changing climate. This study demonstrates, however, that adverse additive genetic correlations among traits may severely retard evolutionary change.

It could be argued that species will persist in the face of global warming, because fossil evidence indicates that many taxa have survived through numerous episodes of climate

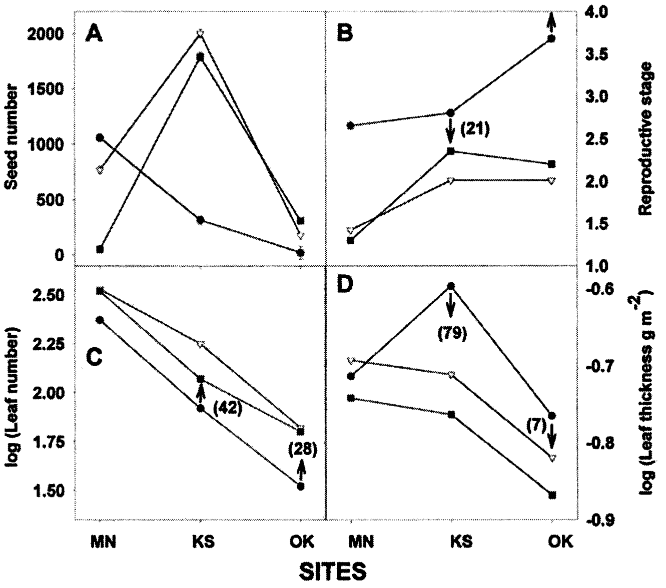

Fig. 3. Least-squares means and standard errors (very small) of (**A**) fecundity, (**B**) reproductive stage, (**C**) log (leaf number), and (**D**) log (leaf thickness) for MN (circles), KS (triangles), and OK (squares) populations reciprocally planted in each of MN, KS, and OK sites (*26*). The direction of the evolutionary trajectory is indicated with an arrow, and the number of generations required to achieve the phenotypic mean of the local population is shown in parentheses for the MN population reared in KS and OK (only leaf number in KS is statstically significant).

Table 2. Additive genetic correlations, r_A, among traits. The concordance of r_A with the direction of the vector of selection on pairs of traits is given in parentheses (R = reinforcing; A = antagonistic).

		MN population		KS population		OK population	
		Leaf number	Leaf thickness	Leaf number	Leaf thickness	Leaf number	Leaf thickness
MN site	Reproductive stage	−0.49 (R)	0.46 (R)	−0.91 (R)	0.28 (A)	−0.66 (R)	0.31 (A)
	Leaf number		0.57 (A)		0.13 (R)		−0.05 (A)
KS site	Reproductive stage	−0.51 (R)	−0.73* (A)	0.18 (A)	−1.02 (R)	−0.75** (A)	0.53 (R)
	Leaf number		0.27* (A)		−3.97* (A)		−0.30 (A)
OK site	Reproductive stage	−0.82****(A)	−0.59** (R)	0.69 (R)	−0.52 (A)	−0.63***(R)	0.18 (R)
	Leaf number		0.47** (A)		0.17 (R)		−0.65 (R)

*$P < 0.09$. **$P < 0.05$. ***$P < 0.01$. ****$P < 0.001$.

change in the past. However, historical climate changes were generally much slower (by one or more orders of magnitude) than those predicted for the future (*23, 24*). Slower changes may have provided opportunities for taxa to adapt to climate change while persisting in refuges or shifting ranges to new latitudes despite genetic constraints on adaptive evolution.

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6. The locations of the natural populations were as follows. MN: Kellog-Weaver dunes, Wabasha County, Minnesota; KS: Konza Prairie, Riley County, Kansas; OK: Pontotoc Ridge, Pontotoc County, Oklahoma. *C. fasciculata* is an native annual legume that has limited dispersal; the estimated neighborhood area based on seed and pollen disperal is 16.7 m^2 [C. B. Fenster, *Evolution* **45**, 398 (1991)].
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8. Data from model CGCM1 of the Canadian Climate Center are available at www.cccma.bc.ec.gc.ca/models/cgcm1.shtml, manipulated by VEMAP2. An overview from T. Kittel *et al.*, ("VEMAP Phase II: Overview of VEMAP2 Gridded Climate Time Series for the U.S. National Assessment") is available at www.cgd.ucar.edu/vemap/V2.html (1999).
9. Field-collected seeds were grown under greenhouse conditions and crossed within populations according to nested paternal half-sib crossing designs, with three randomly chosen dams mated to each sire. Forty-eight half-sib families (144 full-sib) were produced within the MN population, 45 half-sib families (135 full-sib) within KS, and 50 half-sib (150 full-sib) within OK.
10. In spring 1998, pedigreed seeds, planted and reared in a greenhouse at the University of Minnesota for 3 weeks, were transplanted into field sites. For the OK site, seeds were planted 1 May and seedlings were transplanted 19 to 21 May at the Robert S. Kerr Environmental Research Center (Ada, OK). For the KS site, seeds were planted 6 May and transplanted 25 to 27 May at the Konza Prairie Research Natural Area (Manhatten, KS). For the MN site, seeds were planted 13 May and transplanted 30 May to 1 June at the University of Minnesota (St. Paul, MN). The planting design (four blocks per site and two replicates of each full-sib family per block) was not fully balanced because of germination failure, seedling mortality in the greenhouse, and planting errors (total plant numbers: MN = 3247, KS = 3360, and OK = 3301). At all sites, seedlings were watered for 5 days after transplantation. The OK site was weeded in June; the KS and MN sites were weeded in July and August. Few plants were damaged by deer (OK, 3.1%; KS, 1.2%). Another 1.9% of the plants at the OK site were lost due to vandalism. Palmer's drought severity index indicated that the climate in MN was drier than normal during the full growing season, KS was dry in April and May but near normal for the rest of the growing season, and OK had drought conditions beginning in April that became severe from July to September and had a record number of consecutive days over 37.8°C.
11. Phenological stages were as follows. 0, died before reproduction; 1, vegetative plant; 2, flowering plant without pods; 3, plant with developing green pods; 4, plant with ripening brown pods; and 5, senescent plant. Leaf thickness (specific leaf area) is leaf area (m^2) divided by dry leaf weight (g).
12. Fecundity is average seed count of three collected pods times total pod number. In cases where seed counts were not available because pods had already dehisced, fecundity was estimated using the average seed count of the other full-sib replicate within the block or, if that was not available, the average seed count of the full-sib family across blocks.
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15. Variance components were restricted to the feasible parameters space (greater than zero). Signficance testing of Cov_{Aij} was done by calculating the log-likelihood ratio (LRT) and testing it against a chi-square distribution with one degree of freedom. LRT = $-2\ (L_o - L_{max})$, where L_o is the log likelihood of the null hypothesis that $\mathrm{Cov}_{Aij} = 0$, and L_{max} is the log likelihood of the full model. LRT is distributed asymptotically as a chi square with *r* degress of freedom, where *r* is the number of parameters specified under the null hypothesis. To conform to the assumptions of multivariate normality, fecundity was log-transformed. Normality was assessed by visual inspection of normal probability plots of residuals from nested analysis of variance (ANOVA) for each population and site combination. Fecundity estimates of zero, which reflect plant death or unsuccessful reproduction, were retained despite distributional problems that they induced, because these observations reflect the process of natural selection. For plants in each population-site combination, fecundity was converted to relative fitness by dividing by the corresponding site- and population-mean fecundity. All other traits were log-transformed except for reproductive stage, where transformation did not improve the fit to normality. To account for patterns of environmental variation within the field plots, block and row within block were included as categorical factors in the models and position within row was included as a continuous covariate in all analyses.
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26. ANOVA test statistics for the population factor (block and row position nested within block are not shown) for each site and trait, corresponding to Fig. 3, are as follows (****P* < 0.001). (A) Seed number: MN site $F_{2,\ 3288} = 240$ ***; KS site $F_{2,\ 3235} = 563$ ***; OK site $F_{2,\ 3252} = 544$ ***. (B) Reproductive stage: MN site $F_{2,\ 2489} = 720$ ***; KS site $F_{2,\ 2527} = 474$ ***; OK site $F_{2,\ 3354} = 1187$ ***. (C) log (Leaf number): MN site $F_{2,\ 2323} = 89$ ***; KS site $F_{2,\ 2484} = 367$ ***; OK site $F_{2,\ 3280} = 595$ ***. (D) log (Leaf thickness g m^{-2}): MN site $F_{2,\ 3051} = 110$ ***; KS site POP $F_{2,\ 3221} = 529$ ***; OK site $F_{2,\ 3190} = 510$.
27. We thank F. Shaw for statistical advice and programming; S.-M. Chang and M. B. Davis for encouragement and comments on the manuscript; the Minnesota and Oklahoma Chapters of the Nature Conservancy and staff at the Konza Prairie Scientific and Natural Area and the Robert S. Kerr Environmental Research Center for logistical support; and M. Etterson, D. Otterson, R. Otterson, A. Mertyl, J. Larson, L. Kinsell, and T. Nguyen for field work. Supported by U.S. Environmental Protection Agency STAR fellowship U 914758-01-2, the Minnesota Center for Community Genetics, the Dayton-Wilkie Funds for Natural History, and the graduate school of the University of Minnesota.

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Direct Interaction of *Arabidopsis* Cryptochromes with COP1 in Light Control Development

Haiyang Wang,[1] Li-Geng Ma,[1,2] Jin-Ming Li,[3] Hong-Yu Zhao,[3] Xing Wang Deng[1,2]*

***Arabidopsis* seedling photomorphogenesis involves two antagonistically acting components, COP1 and HY5. COP1 specifically targets HY5 for degradation via the 26S proteasome in the dark through their direct physical interaction. Little is known regarding how light signals perceived by photoreceptors are transduced to regulate COP1. *Arabidopsis* has two related cryptochromes (cry1 and cry2) mediating various blue/ultraviolet-A light responses. Here we show that both photoactivated cryptochromes repress COP1 activity through a direct protein-protein contact and that this direct regulation is primarily responsible for the cryptochrome-mediated blue light regulation of seedling photomorphogenic development and genome expression profile.**

Arabidopsis uses two major types of photoreceptors, the red/far-red light-absorbing phytochromes (phyA-phyE) and two related blue/ultraviolet-A (UV-A)–absorbing cryptochromes (cry1 and cry2) to monitor the ambient light environment and to control the seedling developmental pattern, photomorphogenesis in the light and skotomorphogenesis in darkness (*1, 2*). Previous studies showed that a group of COP/DET/FUS proteins function as repressors of photomorphogenesis (*3–5*). They achieve their roles by