

Selection for Orchardgrass Seed Yield in Target vs. Nontarget Environments

M. D. Casler,* R. E. Barker, E. C. Brummer, Y. A. Papadopolous, and L. D. Hoffman

ABSTRACT

Simultaneous improvement of forage traits and seed yield in orchardgrass (*Dactylis glomerata* L.) has been problematic because of geographic separation of forage and seed production locations. Previous work has shown that a complex multilocation selection program in forage production environments can increase forage yield as well as seed yield in Oregon. The objective of this experiment was to compare target-environment (TE) and nontarget-environment (NTE) selection approaches for increasing seed yield of orchardgrass in Oregon. Two cycles of recurrent phenotypic selection for panicle seed mass (PSM) and agronomic traits were conducted on four populations in four eastern USA locations (NTE) and one Oregon location (TE). Seed yield was increased in three of four orchardgrass populations by TE selection, averaging 5.1% cycle⁻¹, but was improved by NTE selection in only one of four populations. Conversely, TE selection for PSM and agronomic traits resulted in no changes to forage yield in the eastern USA and Canada, while NTE selection for PSM and agronomic traits increased forage yield in two of four populations, confirming results of a previous study. It appears that the most efficient system for simultaneously improving forage and seed traits of orchardgrass would be to practice selection for forage traits in forage production environments and seed traits in seed production environments, with sufficiently large populations to allow multitrait selection.

MOST FORAGE CROPS, including orchardgrass, have two distinct commodities: forage and seed. Because orchardgrass cannot be grown for forage without first generating seed to be used for planting, these two commodities are inextricably interdependent. As a forage crop, orchardgrass is widely grown from eastern Canada to the eastern and midwestern USA (Christie and McElroy, 1995). Orchardgrass is most widely grown as a seed crop in the Willamette Valley of Oregon, an area uniquely suited for seed production of numerous perennial, cool-season grasses, because of its mild winters, cool summers, and favorable timing of precipitation.

Because forage and seed production environments do not overlap, orchardgrass breeders are located within one or the other region. Because of the expense and inconvenience of distant test sites, orchardgrass breeders have traditionally focused efforts on forage traits if located in a forage production region and seed traits if located in a seed production region. Thus, new cultivars bred in the eastern or central USA are not necessarily good seed producers and vice versa. Genotype \times loca-

tion interaction between the Pacific Northwest and the eastern USA is well documented for total seed yield (TSY) of orchardgrass (Godshalk, 1984; Leudtke, 1984; Stratton and Ohm, 1989). The most successful orchardgrass breeding programs in North America are those that utilize both forage and seed production environments for simultaneous improvement of both commodities (Casler et al., 2000).

Convergent-divergent selection, a method designed to improve regional adaptation, is based on recurrent selection at a number of diverse locations, where seed used to begin each new cycle of selection at a specific location is derived from selections made at a different location (Lonnquist et al., 1979). Using two cycles of convergent-divergent selection at four locations in the central and eastern USA, we previously demonstrated improved Oregon seed yield as a direct result of selection in two of four germplasm pools (Barker et al., 1997). Selection, based on panicle seed mass (PSM) and agronomic traits associated with forage production, also resulted in increased forage yield in these two germplasm pools (Casler et al., 1997a). We concluded that convergent-divergent selection at a range of diverse nontarget locations was responsible for increasing the frequency of a diverse array of alleles for seed production of orchardgrass, resulting in increased seed production in the target environment (Barker et al., 1997). Conversely, single-location selection for the same traits in the same germplasm pools resulted on no gains in Oregon seed yield, likely because of the genotype \times location interaction that exists between Oregon and the eastern USA.

These previous studies provided a critical comparison of convergent-divergent selection with single-location selection as a control, effectively comparing progress for a multistate, collaborative effort vs. one breeder with one selection location. However, these studies did not address the issue of selection in target vs. nontarget environments, providing a direct comparison between the progress that could be achieved by a breeder in Oregon vs. the multistate collaborative effort. To do this, we resampled the original germplasm pools and practiced two cycles of single-location selection at a representative location in Oregon. The objectives of this study were to evaluate and compare two cycles of recurrent phenotypic selection for increased panicle seed mass and agronomic traits using two selection methods: convergent-divergent (multilocation) selection in nontarget environments vs. selection in a single target location.

MATERIALS AND METHODS

Germplasm

Selection was practiced in four orchardgrass base populations, each derived as part of a breeding program in Iowa

M.D. Casler, USDA-ARS, U.S. Dairy Forage Research Center, Madison, WI 53706-1108; R.E. Barker, USDA-ARS, National Forage Seed Production Research Center, 3450 S.W. Campus Way, Corvallis, OR 97331-7102; E.C. Brummer, Dep. of Agronomy, Iowa State Univ., Ames, IA 50010; Y.A. Papadopolous, Agriculture and Agri-Food Canada, Crops and Livestock Research Centre, 440 University Ave., Charlottetown, PEI, Canada C1A 4N6; L.D. Hoffman, Dep. of Agronomy, The Pennsylvania State Univ., State College, PA 16801. Received 13 April 2002. *Corresponding author (mdcasler@facstaff.wisc.edu).

(IA), Missouri (MO), Pennsylvania (PA), or Wisconsin (WI). Population I79DT is a medium-early, 51-clone synthetic derived by two cycles of phenotypic selection for resistance to stem rust (caused by *Puccinia graminis* Pers.:Pers. subsp. *graminicola* Z. Urban), winter survival, and drought tolerance. The germplasm parentage before selection was derived from Iowa clones (47%), Russian accessions (47%), and Romanian accessions (6%). Population MO2 is a six-clone synthetic, whose parents were selected for resistance to stem rust and derived from old pastures in Missouri. Population PLS4 is a composite of the progenies from fourth-cycle selections for resistance to purple leaf spot (caused by *Stagonospora arenaria* Sacc.) (Zeiders et al., 1984). Population WO11 is a composite of equal amounts of germinable seed from 16 cultivars or experimental populations. The 16 sources of WO11 were chosen from among 55 cultivars and experimental populations tested between 1982 and 1984 at Arlington, WI, solely on the basis of high forage yield.

Selection Protocols

The nontarget environment (NTE) selection protocol was applied independently, but identically, to each of the four base populations and was described in detail by Casler et al. (1997b). The essential elements are as follow.

1. Each population was selected for panicle seed mass and other agronomic traits at each of four locations in the central and eastern USA. Selection was practiced in two stages: Stage I reduced the population from 800 to 200 plants per location based on agronomic traits (maternal and paternal selection), while Stage II reduced the population from 200 to 50 plants per location based on panicle seed mass (maternal selection only). There were 50 maternal plants and 200 paternal plants selected at each location.
2. Seeds produced on selected plants at each location were bulked in equal quantities.
3. Location bulks were gathered together at a single location and used to create three-location-bulks to begin the second cycle. Seeds used to begin Cycle 2 were produced on plants selected at the three other locations, ensuring that the progeny of Cycle 2 had parents and grandparents that were selected at two different locations. This approach is termed convergent-divergent selection (Casler et al., 1997b).

The target-environment (TE) selection protocol was identical to the NTE selection protocol with two exceptions. First, selection was practiced only at Corvallis, OR, so that seed bulks of each cycle were simple bulks of all plants selected in that cycle. Second, the agronomic traits that were used in Stage I differed between TE and NTE selection. In TE selection, Stage I selection was for high panicle number and resistance to stripe rust (caused by *Puccinia striiformis* Westend.). In NTE selection, the agronomic traits were plant vigor, heading date, and disease reaction (Casler et al., 1997b). Stage II selection and all other aspects of TE selection were identical to NTE selection as described by Casler et al. (1997b).

Two cycles of TE selection were performed at Corvallis, OR in 1991 through 1994. The first year of each cycle involved transplanting and grow-in of spaced plants. The second year of each cycle involved selection and seed production. The two cycles of TE selection created four C1 and four C2 populations, one for each germplasm pool. A random sample of Syn-1 seed of the eight TE-selected populations and the comparable eight NTE-selected populations (Casler et al., 1997b) was used to establish 16 spaced plantings of 800 plants each at Corvallis,

OR. The C1 plantings were established in 1993 after the completion of Cycle 1 and the C2 plantings were established in 1995 after the completion of Cycle 2 of TE selection. These crossing blocks were isolated from each other and from other orchardgrass by cereal rye (*Secale cereale* L.) borders at a minimum distance of 10 m between blocks. Syn-2 seed was produced on each crossing block in the first year after transplanting by compositing an equal amount of seed from each plant in the crossing block. In addition, fresh seed of the original four germplasm pools was produced by allowing unselected C0 plants in the 800-plant C1 selection nurseries to intercross and produce seed in 1993, 1 yr after the completion of Cycle 1. Thus, each population, including originals, TE's, and NTE's was advanced one generation in an isolated 800-plant crossing block at Corvallis, OR, between 1993 and 1996.

Evaluation of Selection Progress for Forage Production

Seeds of the 20 Syn-2 populations described above, plus six cultivars (Benchmark, Hallmark, Potomac, Dawn, Justus, and Pennlate) were planted at four locations in April 1997. Locations and soil types were: Arlington, WI [43°20' N, 89°23' W; Plano silt loam (fine-silty, mixed, mesic Typic Argiudolls)]; Ames, IA [42°1' N, 93°48' W; Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludolls)]; Rock Springs, PA [40°45' N, 77°52' W; Hagerstown silt loam (fine, mixed, mesic, Typic Hapludalfs)]; Nappan, Nova Scotia, Canada [45°46' N, 64°15' W; elevation 20 m; reddish-brown loam till (Gleyed Brunisolic Gray Luvisol)].

The experimental design was a randomized complete block with four replicates and a split-split-plot randomization restriction. There were five whole plots: I79DT, MO2, PLS4, WO11, and cultivars. Subplots were selection methods (TE vs. NTE) and sub-sub-plots were cycles. Each subplot included a plot of the original germplasm pool (C0). Plots were seeded in drilled rows approximately 10 cm apart. Plot size was 0.9 by 3.0 m at Arlington, Ames, and Rock Springs, and 1.5 by 6.0 m at Nappan. Seed samples of each population were tested for germination and purity using the blowing method of Everson and Hotchkiss (1977). The seeding rate was 13.4 kg pure live seed (PLS) ha⁻¹.

Plots were clipped two or three times during the seeding year. Nitrogen fertilizer was applied in spring 1998 and 1999, and after harvests one and two in 1998 and 1999, at a rate of 90 kg N ha⁻¹. Applications of P and K fertilizer were made according to soil-test results. Plots were harvested three times per year in 1998 and 1999 with a flail-type harvester. A 300- to 500-g subsample of harvested forage was collected and dried at 60°C in a forced-air dryer for dry-matter determination. The entire plot was harvested at all locations except Nappan, for which a 1.0-m swath was harvested from the middle of each plot.

Evaluation of Selection Progress for Seed Production

The 20 populations and six cultivars were planted at Aurora (May 1997) and Corvallis (April 1997), OR for seed production evaluation. The soil types were Willamette silt loam (fine-silty, mixed, superactive, mesic, Pachic Ultic Argixerolls) at Aurora (45°17' N, 122°45' W), and Woodburn silt loam (fine-silty, mixed mesic, Aquultic Agrikerolls) at Corvallis (44°38' N, 123°12' W). Data were collected on plots in 1998 and 1999 at both locations and 2000 at Corvallis.

The experimental design was identical to that described above, except for plot size. Plots were four 7-m rows, spaced 0.45 m within plots and 0.9 m between plots. Alleys between

plot ranges were 6 m wide and maintained as bare soil throughout the experiment. Plots were seeded with 120 PLS m⁻². This seeding rate reflected an average commercial rate of 5 kg PLS ha⁻¹. The plot area was fertilized by soil incorporation of 36 kg N ha⁻¹, 15 kg P ha⁻¹, 30 kg K ha⁻¹, and 16 kg S ha⁻¹ applied as a complete blend before seeding in 1997. Thereafter, fertilizer was applied in split applications; 33 kg N ha⁻¹, 18 kg P ha⁻¹, and 31 kg S ha⁻¹ as ammonium phosphate sulfate in the fall (mid-November 1997, 1998, and 1999) and two applications of 62 kg N ha⁻¹ as urea in the spring (early March and mid-April 1998, 1999, and 2000). Irrigation was applied immediately after seeding and at short intervals thereafter in 1997 for establishment. Irrigation was not applied after 1997. Weeds were controlled with applications of 0.28 kg a.i. ha⁻¹ of bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) plus 0.28 kg a.i. ha⁻¹ MCPA [(4-chloro-2-methylphenoxy)acetic acid] after emergence and 2.24 kg a.i. ha⁻¹ of diuron [*N*-(3,4 dichlorophenyl)-*N,N*-dimethylurea] each fall. Alleys were maintained weed-free by hand, mechanical cultivation, and spot application of glyphosate [*N*-(phosphonomethyl)glycine] as needed.

Plant traits measured each year (1998 and 1999 at both locations, and 2000 at Corvallis) included heading date (DOY when 50% of the panicles in a plot had emerged from the boot); anthesis date (DOY when 50% of the emerged panicles were in anthesis); stripe rust score after anthesis (1 = no rust, 2 = resistant type reaction, 3, and 4 were moderately susceptible reactions, and 5 = very susceptible with large pustules and over 25% of leaf covered); lodging at heading, anthesis, and harvest (scored as 0 = no lodging to 5 = all plants completely lodged); plant height at harvest (average height of the plants in a plot from ground surface to tip of panicle); TSY (full-plot harvest seed yield); and PSM (mass of seed from ten random panicles chosen at time of harvest from each plot by the same individual each year). Seed mass from the 10-panicle sample was added to the cleaned seed mass from the full-plot harvest to determine TSY. The central 5 m of the two internal plot rows were harvested with a small-plot sickle-bar mower equipped with header and conveyor belt so full-plot biomass could be placed in jute bags. Harvest date for each population or cultivar was determined when seed moisture content was approximately 44 to 45 g kg⁻¹ (fresh weight basis), as described by Klein and Harmond (1971). Harvested panicles and biomass were hung from wire lines and allowed to air dry in the field. The 10-panicle samples were hand threshed on rubber-coated rasping blocks and blown clean in a South Dakota blower (Hoffman Mfg., Albany, OR). Mass of 1000 seeds from the 10-panicle sample was determined. Biomass from the full-plot harvest was threshed in

a horizontal-belt thresher. Seed was cleaned through a seed scalper to remove excess straw followed by two passes through an M2B seed cleaner (Crippen Intl., Dallas, TX).

Data Analysis

Data were analyzed by analysis of variance using the split-plot-in-time model (Steel et al., 1996). All factors were assumed to be random, except populations. Selection responses were computed by linear regression of cycle means on cycle number and tested as contrasts within the analyses of variance.

RESULTS AND DISCUSSION

Selection responses showed some inconsistencies across locations and years, indicating genotype × environment interactions. Selection effects that were significant ($P < 0.05$), when averaged across locations and years, were always consistent in sign and generally consistent in magnitude across locations and years. Those selection effects that were not significant, when averaged across locations and years, were highly inconsistent across locations and years indicating either the presence of genotype × environment interactions or lack of selection response. If no clear patterns emerged across locations or years for a particular trait, we took this as evidence for lack of response to selection. Because there were no clear genotype × location or genotype × year interaction patterns, all results are presented as means over locations and years.

Selection responses for increased PSM were highly variable across populations and between the two selection methods (Table 1). Significant positive and negative responses were observed and they generally did not match between the two selection methods, with the exception of MO2 with positive responses for both methods. Selection responses for PSM from NTE selection did not coincide with those observed for the Syn-1 populations (Barker et al., 1997; Casler et al., 1997b). Thus, part of the inconsistency in PSM responses between selection methods may have been due to the random breakup of inter- and intraallelic associations from the extra generation of recombination. Despite this inconsistency, there was a sufficiently consistent trend across populations for TE selection that the pooled response

Table 1. Mean panicle seed mass (PSM) for four orchardgrass populations subjected to two cycles of phenotypic selection for increased PSM using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr at Aurora and 3 yr at Corvallis, OR.

Selection method/ Population				Selection response		
	C0	C1	C2	Absolute	Percentage	P-value
	g panicle ⁻¹			g panicle ⁻¹ cycle ⁻¹	% cycle ⁻¹	
<u>Nontarget environments</u>						
I79DT-NTE	0.601	0.563	0.612	0.005	0.9	0.76
MO2-NTE	0.597	0.663	0.757	0.080	13.4	<0.01
PLS4-NTE	0.621	0.542	0.536	-0.043	-6.9	0.02
WO11-NTE	0.632	0.641	0.595	-0.019	-2.9	0.29
Pooled-NTE	0.613	0.602	0.625	0.006	1.0	0.49
<u>Target environments</u>						
I79DT-TE	0.601	0.629	0.620	0.010	1.6	0.58
MO2-TE	0.597	0.697	0.657	0.030	5.0	0.09
PLS4-TE	0.621	0.608	0.601	-0.010	-1.7	0.56
WO11-TE	0.632	0.660	0.811	0.089	14.1	<0.01
Pooled-TE	0.613	0.648	0.672	0.030	4.8	<0.01

Table 2. Mean seed yield (TSY) for four orchardgrass populations subjected to two cycles of phenotypic selection for increased panicle seed mass using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr at Aurora and 3 yr at Corvallis, OR.

Selection method/ population	C0	C1	C2	Selection response		
				Absolute	Percentage	P-value
				kg ha ⁻¹ cycle ⁻¹	% cycle ⁻¹	
<u>Nontarget environments</u>						
I79DT-NTE	981	948	898	-42	-4.2	0.05
MO2-NTE	1183	1274	1365	91	7.7	<0.01
PLS4-NTE	1056	928	865	-95	-9.0	<0.01
WO11-NTE	1027	1158	1094	34	3.3	0.11
Pooled-NTE	1062	1077	1056	-3	-0.3	0.76
<u>Target environments</u>						
I79DT-TE	981	1167	1036	27	2.8	0.19
MO2-TE	1183	1249	1264	40	3.4	0.05
PLS4-TE	1056	931	1165	55	5.2	0.01
WO11-TE	1027	1145	1217	95	9.2	<0.01
Pooled-TE	1062	1123	1170	54	5.1	<0.01

was significant (Table 1). Thus, selection for PSM in the target environments was generally more successful than in the nontarget environments, despite the use of multiple nontarget locations.

Seed yield responses to NTE selection were reduced in the Syn-2 generation (Table 2) compared to the Syn-1 generation (described by Barker et al., 1997) for all populations except MO2. In the Syn-1 generation, WO11 increased in TSY similar to MO2 (Barker et al., 1997), but declined significantly due to recombination between Syn-1 and Syn-2. For I79DT and PLS4, TSY responses were not significant in Syn-1 (Barker et al., 1997) and significantly negative in Syn-2. Thus, similar to results for PSM, orchardgrass seed yield is highly sensitive to the breakup of inter- and/or intraallelic associations by recombination.

Much of the variation in TSY was associated with PSM, with a phenotypic correlation coefficient, $r = 0.69$ ($P < 0.01$), between the two traits. Increased TSY for MO2 from NTE selection and for MO2 and WO11 from TE selection (Table 2) was due largely to increases in PSM (Table 1). Similarly, decreased TSY of PLS4 from NTE selection was due to decreased PSM. Conversely, increased TSY of PLS4 from TE selection and decreased TSY of I79DT from NTE selection could not be explained by changes in PSM. Thus, other traits, such as seed mass or panicle density can contribute to changes

in TSY as a result of selection. Selection for increased panicle density during Stage I of TE selection may have been responsible for the increased TSY of PLS4.

As with PSM, the pooled response for TSY was significant for TE selection, but not for NTE selection (Table 2). Furthermore, despite the apparently different mechanisms by which TSY was increased in the four populations undergoing TE selection, their selection responses were remarkably homogeneous, lacking significance in only one population, likely due to insufficient replication. Thus, selection for TSY in Oregon is more effective in Oregon than in the eastern USA, despite the use of multiple eastern-USA locations. While multi-location selection, in the form of convergent-divergent selection, can overcome part of this genotype \times location interaction for TSY (between the Pacific Northwest and the eastern USA), it remains less efficient than selection in the target environments per se. Furthermore, the multi-location selection effort required an unprecedented amount of coordination, cooperation, and commitment, a result that is not practical, efficient, or sustainable in a forage-grass breeding program.

Both TE and NTE selection resulted in significant responses to later anthesis for all four populations (Table 3). For NTE selection, these results were as observed previously, in both forage and seed production environments, although the responses were greater in the Syn-1

Table 3. Mean anthesis date for four orchardgrass populations subjected to two cycles of phenotypic selection for increased panicle seed mass using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr at Aurora and 3 yr at Corvallis, OR.

Selection method/ population	Selection response					
	C0	C1	C2	Absolute	Percentage	P-value
	DOY			d cycle ⁻¹	% cycle ⁻¹	
<u>Nontarget environments</u>						
I79DT-NTE	158	160	160	1	0.6	<0.01
MO2-NTE	152	154	154	1	0.7	<0.01
PLS4-NTE	157	160	160	2	1.0	<0.01
WO11-NTE	154	156	158	2	1.1	<0.01
Pooled-NTE	155	157	158	1	0.8	<0.01
<u>Target environments</u>						
I79DT-TE	158	157	160	1	0.6	<0.01
MO2-TE	152	155	154	1	0.7	<0.01
PLS4-TE	157	157	158	1	0.4	<0.01
WO11-TE	154	152	158	2	1.0	<0.01
Pooled-TE	155	155	157	1	0.7	<0.01

Table 4. Mean plant height for four orchardgrass populations subjected to two cycles of phenotypic selection for increased panicle seed mass using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr at Aurora and 3 yr at Corvallis, OR.

Selection method/ population	C0	C1	C2	Selection response		
				Absolute	Percentage	<i>P</i> -value
				cm	cm cycle ^{−1}	% cycle ^{−1}
<u>Nontarget environments</u>						
I79DT-NTE	162	165	160	−1	−0.4	0.53
MO2-NTE	150	156	157	4	2.4	<0.01
PLS4-NTE	157	159	157	0	0.1	0.87
WO11-NTE	160	158	162	1	0.6	0.35
Pooled-NTE	157	160	159	1	0.6	0.05
<u>Target environments</u>						
I79DT-TE	162	159	161	0	−0.2	0.79
MO2-TE	150	157	155	2	1.6	0.02
PLS4-TE	157	162	161	2	1.2	0.06
WO11-TE	160	154	164	2	1.3	0.05
Pooled-TE	157	158	160	2	1.0	<0.01

generation (described by Barker et al., 1997; Casler et al., 1997a,b). Changes in mean anthesis date, measured on the Syn-2 generation, were similar for all populations and for the two selection methods. A trend toward later maturity in selected populations, regardless of the selection criterion, was observed for other orchardgrass populations undergoing half-sib family selection (Casler et al., 2002). Taken together, these results suggest that selection responses toward later anthesis are probably the result of unconscious selection for later maturity. This may have resulted from the delay of seed harvest until the first signs of seed shattering, reducing TSY and PSM on the earliest maturing plants and unconsciously biasing selection toward later maturity. Such an effect would obscure some of the true genetic differences among plants for PSM, perhaps reducing heritability and genetic gains for PSM. The similarity of shifts toward later heading from both TE and NTE (Table 3) and in another study (Casler et al., 2002) supports the hypothesis above. The initial signs of seed shattering is often used as a rapid indicator of seed ripening (Casler et al., 1997b). The shifts in anthesis date were unlikely a result of selection for stripe rust reaction, because the two traits had a positive phenotypic correlation across the 30 populations evaluated in this study ($r = 0.36$, $P < 0.05$). Panicle seed mass was not correlated with

anthesis date, suggesting that any unconscious selection for later anthesis had little or no effect on the observed changes in PSM or TSY, apart from a possible reduction in heritability.

Both TE and NTE selection resulted in some increases in plant height, although this occurred more frequently and more consistently in the populations created by TE selection (Table 4). Increases in plant height were relatively small and may be related to delays in anthesis, also likely caused by unconscious selection. Plant height and anthesis date had a relatively high phenotypic correlation across the 30 populations evaluated in this study ($r = 0.78$, $P < 0.01$).

The evaluation of NTE selection in the Syn-1 generation revealed some coincidental decreases in reaction to stem rust and crown rust (caused by *Puccinia coronata* Cda.) (described by Casler et al., 1997a). This was not observed with stripe rust in this study. One population, I79DT, showed a significant increase in stripe rust reaction from NTE selection (Table 5), but did not show any selection response to stem rust or crown rust in the previous study (Casler et al., 1997a). Although no TE selection responses for stripe rust were significant at $P < 0.05$, they were remarkably similar across populations, resulting in statistical significance across the four populations. This was not surprising, as stripe rust reac-

Table 5. Mean stripe rust reaction for four orchardgrass populations subjected to two cycles of phenotypic selection for increased panicle seed mass using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr at Aurora and 3 yr at Corvallis, OR.

Selection method/ population	Selection response					
	C0	C1	C2	Absolute	Percentage	<i>P</i> -value
	score [†]			units cycle ^{−1}	% cycle ^{−1}	
<u>Nontarget environments</u>						
I79DT-NTE	2.23	2.45	2.50	0.14	6.2	0.02
MO2-NTE	2.35	2.20	2.40	0.02	1.1	0.68
PLS4-NTE	2.68	2.65	2.45	−0.11	−4.2	0.06
WO11-NTE	2.58	2.55	2.60	0.01	0.5	0.84
Pooled-NTE	2.46	2.46	2.49	0.02	0.6	0.61
<u>Target environments</u>						
I79DT-TE	2.23	2.25	2.10	−0.06	−2.8	0.30
MO2-TE	2.35	2.25	2.25	−0.05	−2.1	0.41
PLS4-TE	2.68	2.25	2.45	−0.11	−4.2	0.06
WO11-TE	2.58	2.25	2.35	−0.11	−4.4	0.06
Pooled-TE	2.46	2.25	2.29	−0.08	−3.4	0.01

† Stripe rust score 1 to 5; 1 = none, 5 = most rust, over 25% of leaf covered with large pustules.

Table 6. Mean forage yield for four orchardgrass populations subjected to two cycles of phenotypic selection for increased panicle seed mass using two selection methods (Nontarget vs. Target environments), including selection responses. Means were computed over 2 yr and four locations.

Selection method/ population	C0	C1	C2	Selection response		
				Absolute	Percentage	P-value
				Mg ha ⁻¹ cycle ⁻¹	% cycle ⁻¹	
<u>Nontarget environments</u>						
I79DT-NTE	9.61	9.54	9.72	0.06	0.6	0.51
MO2-NTE	9.00	9.09	9.55	0.27	3.0	<0.01
PLS4-NTE	9.07	8.78	9.10	0.02	0.2	0.84
WO11-NTE	9.00	9.12	9.33	0.17	1.8	0.05
Pooled-NTE	9.17	9.13	9.42	0.13	1.4	<0.01
<u>Target environments</u>						
I79DT-TE	9.61	9.27	9.45	-0.08	-0.8	0.34
MO2-TE	9.00	9.58	9.26	0.13	1.4	0.13
PLS4-TE	9.07	9.74	9.33	0.13	1.4	0.12
WO11-TE	9.00	8.83	9.16	0.08	0.9	0.33
Pooled-TE	9.17	9.35	9.30	0.07	0.7	0.12

tion was one of the agronomic selection criteria for TE selection.

The responses of forage yield to NTE selection were very parallel in Syn-1 (described by Casler et al., 1997a) and Syn-2 (Table 6). Both MO2 and WO11 showed significant increases in forage yield, although the Syn-2 responses were approximately one third as large as observed in the Syn-1 generation (Casler et al., 1997b). The positive and reasonably similar magnitude of forage yield selection responses for NTE selection resulted in a significant pooled response across populations. Conversely, TE selection did not lead to significant changes in forage yield of any population, nor in the pooled response.

CONCLUSIONS

Our previous research demonstrated that it was possible to simultaneously improve forage yield and seed yield of orchardgrass using a multi-location selection system in forage production environments. The current research builds on those observations, by demonstrating that the gains made in Oregon seed yield, by multi-location selection outside of Oregon, were considerably lower and less consistent than the gains that could be made by selection at one location within the Oregon seed production region. Some of the increases in Oregon seed yield resulted from increased PSM, but others were due to other (undetermined) seed yield components. Unlike selection in multiple forage production environments, selection for seed production in Oregon failed to result in changes to forage yield across four forage production locations. This study, combined with results from Barker et al. (1997) and Casler et al. (1997a, b), suggests that the optimal solution to the dual commodity (forage and seed) problem in orchardgrass probably involves simultaneous or tandem evaluation and selection for forage traits in forage production environments and seed traits in seed production environments. Addition of more traits to the selection program will require the use of large population sizes.

The need for an orchardgrass breeding program that routinely utilizes simultaneous and/or tandem selection between Oregon and the eastern USA will be market

driven. Because orchardgrass is a dual-commodity crop, this does not settle the issue of which market—forage or seed—will or should drive the orchardgrass economy. If new cultivars can be successfully marketed with improved forage traits, then convergent-divergent selection for PSM and agronomic traits at multiple and diverse locations (provided resources are adequate) can lead to improvements in forage yield without sacrificing Oregon seed yield. However, if forage producers are not inclined to purchase seed of cultivars with improved forage traits, the orchardgrass market will be exclusively driven by seed producers, eliminating the need for breeding orchardgrass as a forage commodity. Likewise, orchardgrass cultivars with “improved forage traits” should possess sufficient improvements, adequately documented, so as to present a clear choice to forage producers. Selection exclusively in Oregon is unlikely to provide such an improvement.

REFERENCES

- Barker, R.E., M.D. Casler, I.T. Carlson, C.C. Berg, D.A. Sleper, and W.C. Young, III. 1997. Convergent-divergent selection for seed production and forage traits in orchardgrass. II. Seed yield response in Oregon. *Crop Sci.* 37:1054–1059.
- Casler, M.D., C.C. Berg, I.T. Carlson, and D.A. Sleper. 1997a. Convergent-divergent selection for seed production and forage traits in orchardgrass. III. Correlated responses for forage traits. *Crop Sci.* 37:1059–1065.
- Casler, M.D., I.T. Carlson, C.C. Berg, D.A. Sleper, and R.E. Barker. 1997b. Convergent-divergent selection for seed production and forage traits in orchardgrass. I. Direct selection responses. *Crop Sci.* 37:1047–1053.
- Casler, M.D., S.L. Fales, A.R. McElroy, M.H. Hall, L.D. Hoffman, and K.T. Leath. 2000. Genetic progress from 40 years of orchardgrass breeding in North America measured under hay management. *Crop Sci.* 40:1019–1025.
- Casler, M.D., S.L. Fales, A.R. McElroy, M.H. Hall, L.D. Hoffman, D.J. Undersander, and K.T. Leath. 2002. Half-sib family selection for forage yield in orchardgrass. *Plant Breed.* 121:43–48.
- Christie, B.R., and A.R. McElroy. 1995. Orchardgrass, p. 325–334. In R.F. Barnes et al. (ed.) *Forages*. 5th edition. Iowa State Univ. Press, Ames.
- Everson, L.E., and D.K. Hotchkiss. 1977. A comparison of the blowing and hand methods for the purity analysis of *Dactylis glomerata* seed. *Seed Sci. Tech.* 5:451–462.
- Godshalk, E.B. 1984. Genotype, environment, and genotype × environment interaction effects on orchardgrass seed and forage pro-

- duction. M.S. Thesis, The Pennsylvania State Univ., State College, PA.
- Klein, L.M., and J.E. Harmond. 1971. Seed moisture-a harvest timing index for maximum yields. *Trans. ASAE* 14:124-126.
- Leudtke, R. 1984. Breeding orchardgrass for satisfactory Oregon seed yield combined with high Iowa forage yield and quality. Ph.D. diss. (Diss. Abstr. 85-05841) Iowa State Univ., Ames, IA.
- Lonnquist, J.H., W.A. Compton, J.L. Geadelmann, F.A. Loeffel, B. Shank, and F.A. Troyer. 1979. Convergent-divergent selection for area improvement in maize. *Crop Sci.* 19:602-604.
- Steel, R.G.D., J.H. Torrie, and D.A. Dickey. 1996. Principles and procedures of statistics. 3rd ed. McGraw-Hill Book Co., New York.
- Stratton, S.D., and H.W. Ohm. 1989. Relationship between orchardgrass seed production in Indiana and Oregon. *Crop Sci.* 29:908-913.
- Zeiders, K.E., C.C. Berg, and R.T. Sherwood. 1984. Effect of recurrent phenotypic selection on resistance to purple leaf spot in orchardgrass. *Crop Sci.* 24:182-185.