Physiological responses of 6 wheatgrass cultivars to mycorrhizae

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Abstract

The physiological and morphological responses of 6 wheatgrass *(Agropyron)* cultivars to vesicular-arbuscular mycorrhizal inoculation were measured in the greenhouse. These included diploid, tetraploid, and hexaploid cultivars. Plants had up to 94% infection after 4 months. The 2 diploid cultivars *(A. cristatum* cv. 'Fairway' and *A. cristatum* ssp. *puberulum)* formed infection most rapidly, and they also had significantly reduced root biomass and higher water use efficiency with infection. A hexaploid cultivar (*A. cristatum* from U.S.S.R.) produced significantly more tillers with inoculation, while the tetraploid *A. desertorum* cv. 'Nordan' had fewer tillers and wider leaves. Inoculation increased leaf phosphorus concentration in 4 of the 6 cultivars. Carbon dioxide gas exchange rate, transpiration rate, stomatal resistance, and N concentration were not significantly affected by mycorrhizal inoculation for any of the cultivars. The cultivar Nordan had the greatest number of physiological and morphological increases in response to mycorrhizal infection, while *A. cristatum* from Iran (hexaploid) performed most poorly in that it had reduced WUE and no apparent beneficial responses to infection. There was no relationship between ploidy level and mychorrhizal response.

Asian wheatgrasses *(Agropyron)* are frequently used for revegetation of degraded rangelands in the western United States (Johnson 1986). Disturbances such as heavy grazing and erosion tend to reduce vesicular-arbuscular (VA) mychorrhizal fungi (e.g., Powell 1980, Bethlenfalvay and Dakessian 1984, Bethlenfalvay et al. 1985), but limited research has been done on the physiological responses of *Agropyron* species to mycorrhizae. The Asian *Agropyron desertorum* (Fisch. ex Link) Schultes had a greater frequency of arbuscule formation than the North American species *Agropyron spicatum* (Pursh) Scribner & Smith in response to phosphorus fertilization (Caldwell et al. 1985). Work on the related species *Agropyron smithii* Rydberg and *Agropyron dasystachyum* (Hook.) Scribner shows that mycorrhizae may cause significant increases in CO_2, water, and phosphorus uptake, as well as delayed phenology, increased tiller production, and a more prostrate morphology (Allen et al. 1984, Allen and Allen 1986, Miller et al. 1987). It is not known whether the absence of mycorrhizal inoculum might limit *Agropyron* establishment in degraded soils.

A number of different cultivars of Asian *Agropyron* species are commonly used for revegetation. In a series of studies on forage and crop species, different genotypes or cultivars varied in response to mycorrhizae by showing no change to more than a doubling in biomass with infection (Hall et al. 1977, Menge et al. 1978, Azcon and Ocampo 1980, Krishna et al. 1985, Estaun et al. 1987, Lioi and Giovannetti 1987). These studies concluded that differences in mycorrhizal response may be due to differences in the ability of an individual genotype to form infection, to take up P, and form acid phosphatases. Our objectives were to test the effects of mycorrhizal inoculum on several commonly used cultivar as well as wild populations of *Agropyron.*

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Methods and Materials

Six cultivars with known ploidy levels (Asay and Knowles 1985, Dewey 1983) were studied for effects of mycorrhizae (Table 1).

Table 1. Names and ploidy levels of 6 cultivars of *Agropyron* used for studies on response to mycorrhizae.

Name	Ploidy
Agropyron cristatum cv. 'Fairway'	2n=14 (2X)
A. cristatum ssp. *puberulum*	2n=14 (2X)
A. desertorum cv. 'Nordan'	2n=28 (4X)
A. cristatum × *desertorum* cv. 'Hycrest'	2n=28 (4X)
A. cristatum (Iran)	2n=42 (6X)
A. cristatum (USSR)	2n=42 (6X)

Since the *Agropyron* complex is an autoploid series, it is an ideal group to begin studies on the effects of mycorrhizae on genetically related cultivars with different ploidy levels. The *Agropyron* cultivars used in this study originate from different regions in Asia, and some of the cultivars were selected and bred in the United States (Asay 1986). The diploid *A. cristatum* (L.) Gaertner ssp. *puberulum* is a wild type, a cultivar collected in Azerbaijan in 1955 with no further selection, while *A. cristatum* cv. 'Fairway' is a diploid selected from a Siberian introduction and was released in 1932. *A. desertorum* cv. 'Nordan' is a standard type tetraploid cultivar released in 1953, and its parentage was originally from the cold dry plains of the U.S.S.R. Hycrest, a tetraploid hybrid cultivar, was released in 1984. The parental germplasm was generated by crossing induced tetraploid *A. cristatum* with natural tetraploid *A. desertorum* (Asay and Knowles 1985). One hexaploid population of *A. cristatum* was collected at the Iran-Turkey border, and it is a wild type. The other hexaploid *A. cristatum* was collected from Kazakhstan in the USSR and is also a wild type. These 6 cultivars represent both commonly planted (Fairway, Nordan, Hycrest) and wild cultivars.

With the exception of the recently released Hycrest, each of these cultivars was planted in silty clay loam during 1983 at Evan's Farm, ca. 5 km south of Logan, Utah (Dewey 1988). Soil and root samples were taken from each cultivar in May, 1986. Two samples were collected from each of 5 plants per cultivar using a 2 cm diameter × 10 cm soil corer, for a total of 10 cores from each cultivar. The roots were washed and stained with trypan blue (Kormanik et al. 1980) and 50 1-mm root segments from each plant were scored under the microscope at 100 × power for presence or absence of VA mycorrhizal infection. A root segment was considered infected if it contained hyphae, arbuscules, or vesicles. Percentage infection for a plant was based on the number of root segments with infection out of a random sample of 50 segments. Spores were separated by sucrose flotation (Allen et al. 1979). The spores were extracted from 5-g soil samples and then counted under the microscope at 40 × power. Spore densities were

expressed as number per g dry soil.

Greenhouse experiments were conducted to determine the physiological responses of the 6 *Agropyron* cultivars to mycorrhizal infection. The potting soil was collected from approximately the top 10 cm of sagebrush-semidesert in Curlew Valley, north-central Utah (West 1983), an area with extensive planted stands of *A. desertorum*. Soil analyses indicated 20.0 (0.5 S.E., n = 10) mg/kg Olsen bicarbonate extractable P, 1.09 (0.05) mg/kg total Kjedahl N, 5.8 (0.3) % organic matter, pH of 8.28, and electrical conductivity of 0.72 umho/cm. The texture was a silty loam. The mycorrhizal spores were identified using the manual of Schenck and Perez (1988) as primarily *Glomus fasciculatum* (Thaxter sensu Gerdemann) Gerdemann & Trappe and *G. macrocarpum* Tul. & Tul., with less abundant *G. microcarpum* Tul. & Tul., *G. desertícola* Trappe, Bloss & Menge, *G. occultum* Walker and an unidentified *Glomus* spp. Spore densities (0–20/g) and root infection (0–10%) in this field site were extremely low during the 1986 and 1987 growing seasons. Greenhouse bioassays produced little infection from spores or soil, and microscopic observations of the spores showed most to be hollow, possibly parasitized spores (Di 1988). To concentrate inoculum for the pot experiments, root segments with adhering rhizosphere soil were collected in spring 1987 from a lightly grazed *A. desertorum* area in Curlew Valley. This *A. desertorum* stand was genetically most similar to the cultivar Nordan (D. Dewey, pers. comm.).

After steam sterilization (24 hr at 100° C), the soil was placed in 1-liter styrofoam pots. There were 11 replicate plants of each of the 6 cultivars in each mycorrhizal and nonmycorrhizal treatment. For the VA mycorrhizal treatment pots, the middle soil layer contained 1 cm of inoculum (root segments with adhering soil). For the nonmycorrhizal treatment pots, the middle layer was 1 cm steam-sterilized inoculum. The final density after thinning seedlings was 1 plant per pot.

Using roots as inoculum introduces microorganisms other than mycorrhizal fungi, and is not as desirable as the use of surface sterilized mycorrhizal spores because of possible effects of these microorganisms on the growth of the plants. As mentioned above, viable spores were not produced to perform the necessary control experiments. However, numerous control experiments have been performed on related grass species with some of the same fungal species. For instance, the use of root, soil, or surface-sterile spore inocula did not significantly change the magnitude or direction of the physiological responses of *Agropyron smithii* and *Bouteloua gracilis* to mycorrhizae (Allen et al. 1981, 1984; Allen and Allen 1984). Recently completed experiments show that the addition of a soil filtrate (as a control for other microorganisms in the nonmycorrhizal treatment) had no effect on plant growth (Cannon et al. 1990). In the same experiment we compared the species composition of colonizing saprophytic soil fungi of the nonmycorrhizal treatment to fungi in the mycorrhizal treatment (using roots plus adhering soil as inoculum) in a 3-mo. pot experiment. There was 87% similarity of fungal species in the 2 treatments using Sorenson's index (based on species presence/absence). When only the most abundant fungi were considered, the similarity was 100%. Given these data and the conclusions of the previous experiments on grasses, we feel that the results reported here are due primarily to mycorrhizal fungi rather than other soil microorganisms.

Soil moisture was monitored with a thermocouple psychrometer buried in the middle of 2 pots from each treatment, and was maintained between –0.5 and –2.0 MPa by adding measured amounts of water at 2-day intervals. The plants were maintained at approximately 25° C day and 20° C night temperatures under natural daylength, and were harvested after 16 weeks of growth.

The following measurements were made on inoculated and uninoculated plants of each cultivar: (1) leaf water potential, (2) rate of CO_2 exchange and transpiration, (3) N and P concentrations in shoot and root, (4) dry mass, (5) number of tillers, (6) leaf width, and (7) percent root infection.

Leaf water potential and gas exchange were measured during the last 6 weeks of growth on at least 3 plants per treatment of each cultivar, using the same leaf stage for each measurement. A nitrogen pressure chamber (P.M.S. model 1000) was used to measure leaf water potential and an Analytical Development Company Portable Leaf Chamber Analyzer system was used to measure transpiration, CO_2 exchange rate, and stomatal conductance under ambient environmental conditions. Measurements were initiated in well-watered soils and taken daily until leaves began to wilt. Two plants from each treatment were harvested at 5- and 10-week intervals, leaving 7 plants for the final harvest at 16 weeks. At each harvest the percentage root infection and shoot and root biomass were assessed. In addition, tiller number of each plant was counted periodically and at the end of the experiment. Leaf width was measured in conjunction with the gas exchange experiments.

After harvesting, the plants were oven-dried at 65° C and weighed. The P and N concentrations in shoots and roots of both mycorrhizal and nonmycorrhizal plants were examined from 7 plants of each cultivar at the end of the greenhouse experiment. Roots and shoots were digested in acid (Thomas et al. 1967) and P and N detected colorimetrically. Carbon isotope discrimination, expressed as $\delta^{13}C$ (representing the $^{13}C/^{12}C$ isotope ratio) was measured on the final harvested plants with stable isotope analysis on a mass spectrometer (in the laboratory of J. Ehleringer, University of Utah). This ratio gives an integrated estimate of water use efficiency (WUE) over the lifetime of the plant. A more negative $\delta^{13}C$ value indicates lower WUE, which is correlated with less ^{13}C uptake during its lifetime (Farquhar and Richards 1984, Ehleringer et al. 1986). In addition, WUE was calculated from the instantaneous gas exchange measurements.

Statistical analyses were performed as *t*-tests to compare mycorrhizal and nonmycorrhizal plants or ANOVA followed by a least significant difference test ($L.S.D._{0.05}$) to compare mycorrhizal infection among cultivars.

Results

There were some differences in spore numbers and root infection among some of the 5 cultivars growing in the field at Evan's Farm (Table 2). *Agropyron cristatum* (Iran) had the lowest root infection, although the range of infection among the cultivars was small (28–38%). *A. cristatum* cv. Fairway had the lowest spore count. There were no relationships between ploidy level and % infection or spore counts. These data are presented to show the comparative levels of infection that these cultivars may achieve under field conditions.

Table 2. Spore numbers and root infection of 5 *Agropyron* cultivars in the field.

Cultivar	Ploidy	root infection (%)	Spores/g soil
Fairway	2X	35 a	10 b
puberulum	2X	30 ab	23 ab
Nordan	4X	32 ab	30 a
Iran	6X	28 b	26 ab
USSR	6X	38 a	24 ab

Means in a column followed by different letters indicate significant differences at $P<0.05$.

In the greenhouse experiments, the 6 cultivars each had different responses to mycorrhizal inoculation. Total dry mass of mycorrhizal plants at the final harvest was significantly reduced compared to the uninoculated plants for *A. cristatum* ssp. *puberulum* and *A. cristatum* cv. Fairway (Fig. 1). In both cases the reduction

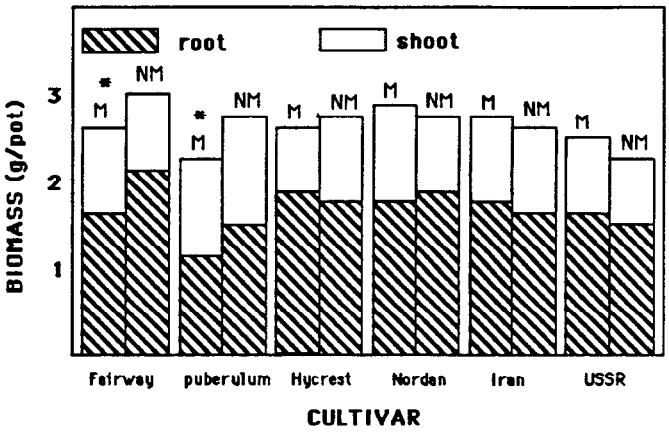

Fig. 1. Root and shoot dry mass of mycorrhizal (M) and nonmycorrhizal (NM) plants of 6 cultivars of *Agropyron* in the greenhouse. * indicates significant differences ($P<0.05$) between mycorrhizal and nonmycorrhizal plants using a *t*-test.

could be attributed to lower root mass, with no significant difference in shoot biomass. There were no significant differences in root or shoot mass between the treatments for any of the other cultivars.

The average tiller number of mycorrhizal plants at the final harvest was significantly higher than that of the uninoculated plants for *A. cristatum* (USSR) (Fig. 2). By contrast, inoculated *A. desertorum* cv. Nordan was lower in tiller production than uninoculated plants. The other 4 cultivars showed no difference in tiller

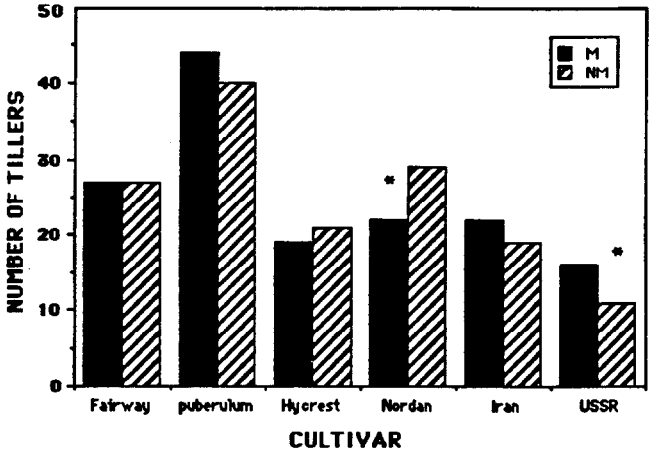

Fig. 2. Number of tillers per plant produced by mycorrhizal (M) and nonmycorrhizal (NM) plants of 6 cultivars of *Agropyron* in the greenhouse. * indicates significant differences ($P<0.05$) between mycorrhizal and nonmycorrhizal plants.

production with mycorrhizae. Only the inoculated *A. desertorum* cv. Nordan had a significantly wider leaf than uninoculated plants (Fig. 3). The other 5 cultivars showed no difference between the 2 treatments.

Four of the cultivars, *A. cristatum* ssp. *puberulum*, *A. cristatum* cv. Hycrest, *A. desertorum* cv. Nordan and *A. cristatum* (USSR), had significantly higher P concentrations in mycorrhizal than nonmycorrhizal plants, while the P concentration in shoots of *A. cristatum* cv. Fairway and *A. cristatum* (Iran) were not different between the 2 treatments (Fig. 4). Phosphorus concentrations in roots were not statistically different between the 2 treatments for any of the 6 cultivars (Fig. 4).

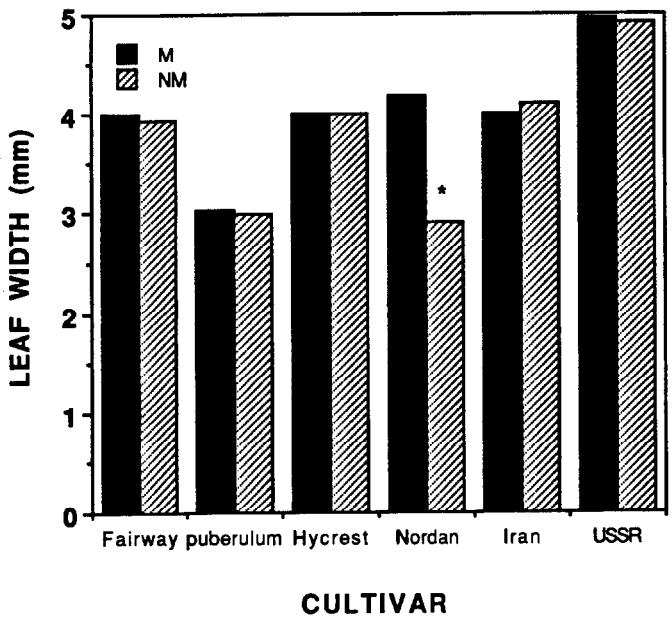

Fig. 3. Leaf width of mycorrhizal (M) and nonmycorrhizal (NM) plants of 6 cultivars of *Agropyron* in the greenhouse. * indicates significant differences ($P<0.05$) between mycorrhizal and nonmycorrhizal plants.

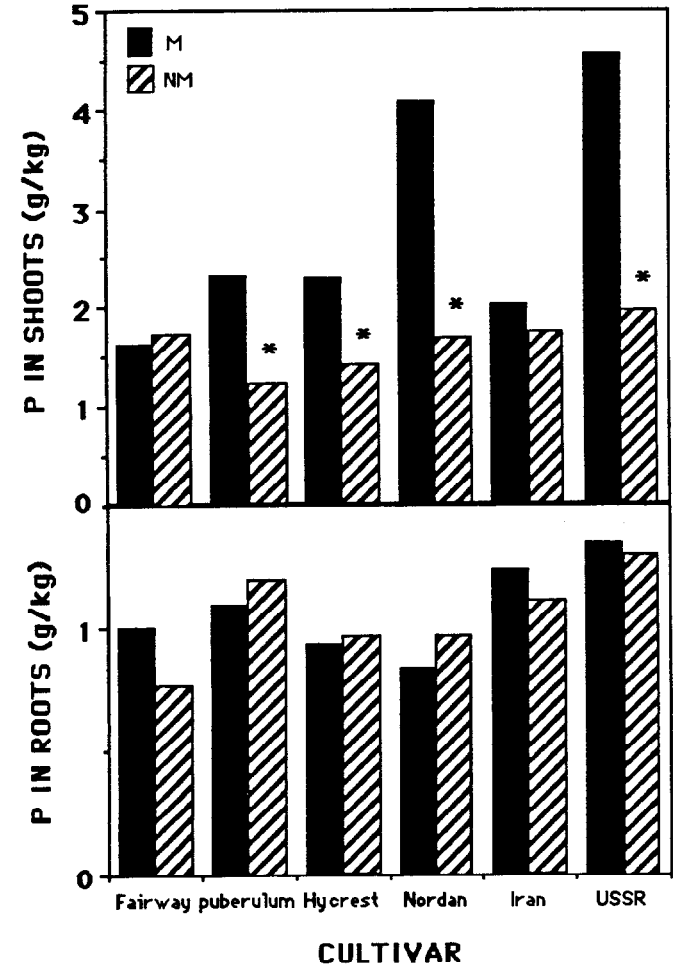

Fig. 4. Phosphorus concentrations in roots and shoots of mycorrhizal (M) and nonmycorrhizal (NM) plants of 6 cultivars of *Agropyron in the greenhouse. * indicates significant differences ($P<0.05$) between mycorrhizal and nonmycorrhizal plants.

There were no differences in N concentrations due to mycorrhizae for shoots or roots of any of the cultivars. The mean value of leaf N, averaged for the mycorrhizal and nonmycorrhizal treatments, was 11.2 mg/kg for Fairway, 10.6 each for *puberulum* and Hycrest, 10.3 for Nordan, 12.3 for Iran, and 14.4 mg/kg for the USSR cultivar ($L.S.D._{0.05}$ = 2.5). Thus, the USSR cultivar had significantly higher leaf N than all but the Iran cultivar.

The water use efficiency, based on $\delta^{13}C$, was higher with mycorrhizal infection for 3 of the cultivars (Fairway, *puberulum,* and Nordan, Table 3). Mycorrhizae reduced WUE using this integrative, longterm measure for the Iran cultivar, and the other 2 were

Table 3. Water use efficiency, means and S.E., of 6 cultivars of *Agropyron* expressed as $\delta^{13}C$ and moles H_2O/CO_2. Means and (S.E.) are given for mycorrhizal (M) and nonmycorrhizal (NM) plants.

	$\delta^{13}C$		moles H_2O/CO_2	
Cultivar	M	NM	M	NM
Fairway	-28.15 (0.29)	-28.53* (0.04)	520 (32)	570 (63)
puberulum	-29.06 (0.15)	-29.70* (0.50)	n.d.	n.d.
Hycrest	-27.90 (0.60)	-27.70 (0.92)	617 (48)	589 (47)
Nordan	-27.94 (0.23)	-28.37* (0.13)	659 (84)	702 (51)
Iran	-27.87* (0.39)	-27.05 (0.10)	628 (41)	688 (62)
USSR	-27.07 (1.19)	-27.15 (0.44)	596 (50)	631 (56)

* = significantly lower WUE at $P<0.05$. using a t-test to compare M (mycorrhizal) and NM (nonmycorrhizal) plants. n.d. = no data.

not significantly changed. Calculations of WUE derived from instantaneous gas exchange measurements showed no significant changes with infection for any of the cultivars (Table 3).

There were no statistical differences in CO_2 exchange rates, transpiration rates, or stomatal resistance due to mycorrhizal infection for any of the 6 cultivars in wet or dry soils. There were also no significant differences in CO_2 exchange or transpiration among the 6 cultivars, using multiple observations on the 7 replicates of each treatment at varying water potentials. The values for data collected from all the cultivars ranged from a low of 4.0 umoles CO_2 m^{-2} sec^{-1} and 2.0 mmoles H_2O m^{-2} sec^{-1} at -44 MPa xylem water potential, to a high of 18.0 umoles CO_2 m^{-2} sec^{-1} and 11.0 mmoles H_2O m^{-2} sec^{-1} at -17 MPa.

Root infection of the 6 cultivars showed some significant differences at the 5 and 10 week sampling periods. The 2 diploid cultivars, *A. cristatum* cv. Fairway and *A. cristatum* ssp. *puberulum,* formed significantly higher infection percentages at 5 and 10 weeks, respectively, than the other cultivars (Fig. 5). At 16 weeks the root infection was similar among the 6 cultivars, ranging from 80 to 94% (Fig. 5). Uninoculated plants had no mycorrhizal infection. The high percent infection in the greenhouse contrasts with the field grown plants which had up to 38% infection (Table 2), and may be due to higher inoculum density and more ideal growth conditions.

In summary, the morphological and physiological responses of the 6 cultivars to mycorrhizal inoculation showed significant increases or decreases for about 22% of the measurements in all the cultivars combined (Table 4). Ploidy level was apparently not related to mycorrhizal response, as the 2 cultivars within each ploidy level showed dissimilar response. For instance, USSR 6X had only increased or no significant physiological response to infection, while Iran 6X had one decrease but no increases.

Discussion

A decreased physiological or morphological response to mycorrhizal infection is often interpreted to be negative to plant growth, but is not necessarily so. For instance, both diploid cultivars had reduced root dry mass with infection, but this is only detrimental to the plant if the external mycorrhizal hyphal length cannot compen-

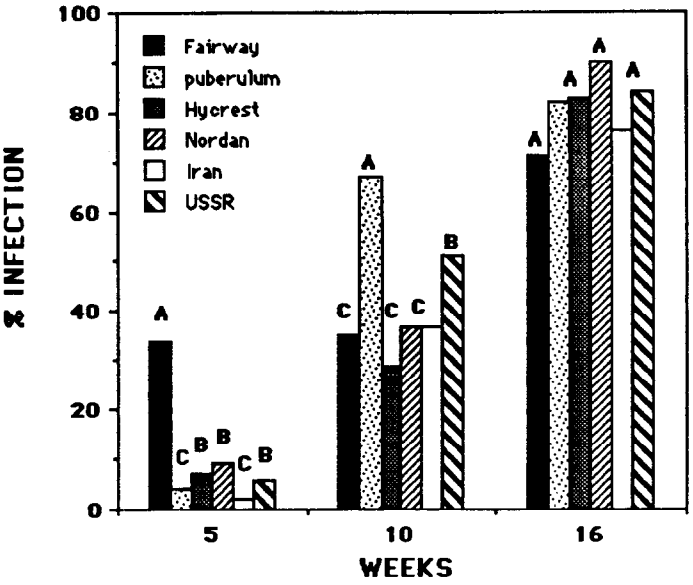

Fig. 5. Percent mycorrhizal infections of inoculated plants of 6 cultivars of *Agropyron* at 3 times during the growth period in the greenhouse. Different letters denote significantly different means within each sample time using the $L.S.D._{0.05}$. Uninoculated plants were not infected.

Table 4. Summary of physiological responses of 6 cultivars of *Agropyron* to mycorrhizal infection.

Cultivar	Fair-way	*puber-ulum*	Hycrest	Nordan	Iran	USSR
Ploidy	2X	2X	4X	4X	6X	6X
Biomass						
shoots	0	0	0	0	0	0
roots	–	–	0	0	0	0
Phosphorus						
shoots	0	+	+	+	0	+
roots	0	0	0	0	0	0
Nitrogen						
shoots + roots	0	0	0	0	0	0
Tiller count	0	0	0	–	0	+
Leaf width	0	0	0	+	0	0
WUE (δ ^{13}C)	+	+	0	+	–	0
CO_2 exchange	0	0	0	0	0	0
Transpiration	0	0	0	0	0	0

+ = increase with infection, – = decrease, 0 = no significant change.

sate by performing some of the absorptive functions of the root (Read 1984). Reduced root mass was apparently not detrimental to either of these cultivars, as both had increased WUE and one *(puberulum)* also had increased leaf P. The cultivar Nordan had fewer tillers with infection, but apparently compensated for this by producing wider leaves. The Iran cultivar was the only one that had only a reduction in response and no increases with infection, but whether its survival is also reduced by having reduced WUE can only be determined by experimentation.

The physiological responses of all 6 *Agropyron* cultivars to VA mycorrhizae were relatively small, but they were similar in magnitude to responses of native North American cool-season grasses, including the related species *Agropyron smithii* and *A. dasystachyum* (Allen et al. 1984; Allen and Allen 1986, 1988; Duce 197; Miller et al. 1987). Reductions in response to infection were also found in several of these studies, and were in some cases related to soil P. *Agropyron smithii* had increased biomass with inoculation in low P soils (2–6 mg/kg P), but had no significant change in mass

with inoculation in high P soils (20–30 mg/kg P) (Duce 1987, Miller et al. 1987). Extractable soil P was relatively high (20 mg/kg) in our greenhouse experiment, but high infection percentages were formed and 4 of the cultivars had increased P concentrations with infection. The reduced root mass of the 2 diploid cultivars with infection may be related to the high percent infection they formed early during their growth. The fungus may have acted as a carbon drain on the maturing seedlings compared to the other cultivars (e.g., Bethlenvalvay et al. 1982).

Mycorrhizal infection resulted in an increased number of tillers for the USSR cultivar, but a decreased number for Nordan. Miller et al. (1987) reported a positive relationship between tiller production and inoculation in *A. smithii* in their high P soil. A similar positive association between tiller production and mycorrhizae was previously reported for wheat (Ellis et al. 1985). In the study of Miller et al. (1987) increased tiller number was associated with decreased leaf height. In our study, decreased tillering of Nordan following infection was accompanied by increased leaf width and no change in biomass.

There have been few attempts to measure WUE of mycorrhizal plants. The WUE efficiency, as inferred by $\delta^{13}C$, generally increased, but in other cases decreased or stayed the same. Allen et al. (1981, 1984) indicated no significant change in WUE of mycorrhizal *Agropyron smithii* and *Bouteloua gracilis,* but these calculations were made with instantaneous gas exchange measurements. Whether mycorrhizae act to increase or decrease WUE depends on their separate effects on roots and leaves. Root surface area determines the rate at which water may be absorbed from the soil while such parameters as leaf area and thickness, stomatal control, density of photosynthetic units, and others determine CO_2 exchange rates (Allen et al. 1981).

The *Agropyron* cultivars are likely to be facultatively mycorrhizal because they showed relatively small responses to infection. However, even relatively small changes in physiology, whether they appear beneficial or detrimental to the plant, are likely to be important to longterm plant survival (Allen and Allen 1986). Mycorrhizal fungi reinvade disturbed arid soils within one or a few growing seasons (Allen and Allen 1980, Waaland and Allen 1987, Warner et al. 1987) if an inoculum source is nearby. If mycorrhizae are not considered, plant breeding and selection practices may produce varieties that do not respond appropriately to the fungal infection. These grasses are often planted in soil with at least some mycorrhizal inoculum, and are subject to mycorrhizal colonization early during their life span. Therefore, the selection of cultivars with desirable responses to mycorrhizae may be important to successful revegetation. Since these are introduced cultivars, their mycorrhizal responses and fungal associates evolved under different environmental conditions. Research on their mycorrhizal associations from their native habitats may provide a further understanding of the particular responses observed in our study.

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