Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis[1]

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To supplement previous studies, wheat ancestors with the A, S(B), D, and AB genomes and modern spring and winter wheat cultivars were vernalized for 42 days in a growth chamber prior to transplanting and growth in a greenhouse for 14 weeks. One-half of the seedlings were inoculated with a mixture of equal numbers of spores of six vesicular–arbuscular mycorrhizal fungi at transplanting. Dry weights of plants and component parts were determined. Percent colonization of roots was determined microscopically. Growth response and mycorrhizal dependence were calculated. However, no mycorrhizal dependence was observed in *Triticum monococcum* PI 266844 and PI 355520 (A genome), *Aegilops speltoides* 1773 (S(B) genome), or in the AB genome ancestors *Triticum carthlicum* 2825, *Triticum polonicum* 2808, *Triticum dicoccum* 1165, *Triticum pyramidale* 2809, *Triticum orientale* 2805, *Triticum paleocolchicum* 2807, and *Triticum persidum* 2811 and 2812. Mycorrhizal dependence in the D genome ancestors was more variable. *Triticum tauschii* var. *typica* accessions 1649, 1691, 2378, 2448, 2492, 2495, 2528, 2541, and 2567 lacked dependence, whereas *T. tauschii* var. *meyeri* 2529 and var. *strangulata* 2377 and 2452 were dependent on mycorrhizal symbiosis. The spring wheat cultivars Chinese Spring 3008, Spelta 2603, Pavon 76 2980, and Norin 29 3025 and the winter wheat cultivars TAM 200, Wrangler, Saluda, and Karl were not dependent on mycorrhizae, whereas winter wheat cultivars TAM 107 and Century were dependent. When these data are synthesized with previously tested ancestors, landraces, and cultivars, it appears that both dependent and nondependent diploid ancestors with the A, S(B), and D genomes existed, but dependence was lost in tetraploid ancestors. Since no dependence on mycorrhizae has been demonstrated in any AB genome ancestors, the presence of dependence in modern cultivars of the hexaploid ABD genome is probably derived from the D genome. The consistent dependence of wheat cultivars released before 1950 suggests that modern breeding practices have reduced dependence on mycorrhizal symbiosis. The implications of having mycorrhizal colonization in the absence of mycorrhizal dependence (benefit) are discussed.

Key words: pathogenesis, growth response, vesicular–arbuscular mycorrhizae.

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Afin de compléter leurs études antérieures les auteurs ont utilisé des ancêtres du blé possédant les génomes A, S(B), D et AB ainsi que des cultivars modernes de blé de printemps et d'hiver; les plants ont été vernalisés pendant 42 jours en chambre de croissance avant de les transplanter et de les cultivar en serre pendant 14 semaines. Au moment de les transplanter, la moitié des plantules ont été inoculées avec un nombre égal de spores appartenant à six espèces de champignons mycorhiziens à vésicules et arbuscules. Les poids secs des plants et de leurs parties ont été mesurés. Le pourcentage de colonisation racinaire a été mesuré au microscope. La réaction de croissance et la dépendance mycorhizienne ont été calculées. Aucune dépendance mycorhizienne n'a été observée chez le *Triticum monococcum* PI 266844 et PI 355520 (génome A), l'*Aegilops speltoides* 1773 (génome S(B)), ou chez les ancêtres du génome AB, chez le *Triticum carthlicum* 2825, le *Triticum polonicum* 2808, le *Triticum dicoccum* 1165, le *Triticum pyramidale* 2809, le *Triticum orientale* 2805, le *Triticum paleocolchicum* 2807, et le *Triticum persicum* 2811 et 2812. La dépendance mycorhizienne chez les ancêtres du génome D est plus variable. Les accessions 1649, 1691, 2378, 2448, 2492, 2495, 2528, 2541, et 2567 du *Triticum tauschii* var. *typica* ne montrent pas de dépendance, alors que les *T. tauschii* var. *meyeri* 2529 et var. *strangulata* 2377 et 2452 dépendent de la symbiose mycorhizienne. Les cultivars de blé de printemps Chinese Spring 3008, Spelta 2603, Pavon 76 2980 et Karl ne dépendent pas des mycorhizes, alors que les cultivars de blé d'hiver TAM 107 et Century sont dépendants. Lorsque ces données sont synthétisées, avec celles des cultivars, races et ancêtres précédemment étudiés, il semble que des ancêtres diploïdes dépendants aussi bien que non-dépendants, possédant les génomes A, S(B) et D, ont existé, mais la dépendance n'a pas été perdue chez les ancêtres tétraploïdes. Puisqu'aucune dépendance mycorhizienne n'a été démontrée chez les ancêtres du génome AB, la présence de dépendance chez les cultivars comportant le génome ABD héxaploïde a probablement dérivé à partir du génôme D. La dépendance usuelle des cultivars de blé introduits avant 1950 suggèrent que les pratiques d'amélioration génétique modernes ont réduit la dépendance mycorhizienne. Les auteurs discutent les implications d'une colonisation mycorhizienne en absence de dépendance mycorhizienne (bénéfices).

Mots clés : pathogénèse, réaction de croissance, mycorhizes à vésicules et arbuscules.

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Introduction

Bread wheat (*Triticum aestivum* L., $2n = 42$, genomes AABBDD) is a species resulting from spontaneous chromosome doubling in a natural hybrid between *Triticum turgidum* ($2n = 28$, AABB) and *Triticum tauschii* ($2n = 14$, DD). The process, known as amphiploidization, that gave rise to bread wheat occurred near the southern to southwestern coast of the Caspian Sea about 6000 years ago. *Triticum turgidum*, which includes wild and cultivated emmer as well as durum wheat, is itself an amphiploid between einkorn wheat (*Triticum monococcum*, $2n = 14$, AA) and another diploid species. The donor of the B genome of *T. turgidum* no longer exists, but there are similarities between the B genome and the S and G genomes, carried by *Aegilops speltoides* (SS) and *Triticum araraticum* (AAGG), respectively. *Triticum turgidum* probably evolved from *T. araraticum*, with replacement of the latter's cytoplasm and one chromosome ($4A^t$) by ones from a third, unknown species (Gill and Chen 1987).

Since wheat is a major food staple for much of the world, considerable scientific effort is aimed at yield improvement and more recently at yield sustainability. The potential for wheat yields to be improved under low-input agriculture by management of mycorrhizal symbiosis is therefore of considerable importance. Previous studies of this symbiosis in wheat have described considerable variability in whether wheat was colonized by the fungal symbionts (Asai 1934; Jakobsen and Nielsen 1983; Trent *et al.* 1988; Hetrick and Bloom 1983; Yocum *et al.* 1985; Dodd and Jeffries 1986). Even when wheat is colonized, the ability of the symbiosis to improve biomass and yield has varied. The variable response of wheat to the symbiosis has been attributed to the nutrient-absorbing efficiency of the fungal symbiont (Vierheilig and Ocampo 1991; Hetrick *et al.* 1992), fertility of the soil (Jakobsen and Nielson 1983; Young *et al.* 1985), timing of colonization (Hetrick *et al.* 1984), and genotype of the cultivar (Azcon and Ocampo 1981; Hetrick *et al.* 1992).

Using a mixture of fungal symbionts known to infect wheat, and a soil low in fertility, Hetrick *et al.* (1992) demonstrated that old hexaploid wheat landraces and older cultivars display more consistent and higher growth responses to the symbiosis than modern cultivars. They suggested that germ plasm selection under fertilized conditions could have reduced the frequency of genes for mycorrhizal dependence in wheat. In studies of wheat ancestors, Kapulnik and Kushnir (1991) suggested that factors limiting mycorrhizal dependence in wheat are found among the A and B genomes but are epistatic to the more consistently dependent D-genome contributors. In contrast, the subsequent study by Hetrick *et al.* (1992) observed strong and consistent dependence on mycorrhizal symbiosis among the A- and S- (B and G) genome contributors and no significant dependence among the two D-genome contributors assessed. Given the considerable dependence on mycorrhizae of the A- and S-genome contributors, the absence in tetraploid ancestors of the AG and AB genomes was enigmatic. Also, given the absence of mycorrhizal dependence in the D-genome contributors and among the tetraploid wheat ancestors, the presence of mycorrhizal dependence in hexaploid (ABD genome) wheats was also difficult to explain.

To resolve some of the questions arising from the previous study and some of the inconsistencies between the results of Hetrick *et al.* (1992) and Kapulnik and Kushnir (1991), a range of other wheat ancestors was evaluated in the present study. In particular, the mycorrhizal dependence of a wide range of A-, B-, AB-, and D-genome contributors as well as other hexaploid wheat cultivars was tested. A synthesis of the mycorrhizal dependencies of the wheat ancestors was developed from the previous (Hetrick *et al.* 1992) and present studies.

Materials and methods

Soil preparation

Native prairie soil, a Chase silty clay loam, fine montmorillonitic mesic Aquic Argiudoll, was freshly collected from Konza Prairie Research Natural Area, Manhattan, Kans. This soil had a pH of 6.2 and contained 10 $mg \cdot kg^{-1}$ (Bray 1) P, 307.3 $mg \cdot kg^{-1}$ K, 15.0 $mg \cdot kg^{-1}$ NO_3, 11.9 $mg \cdot kg^{-1}$ NH_4, 1.8 $mg \cdot kg^{-1}$ Zn, 36.0 $mg \cdot kg^{-1}$ Fe, and 3.8% organic matter, as determined by the Kansas State University Soil Testing Laboratory (Manhattan, Kans.). The soil was steamed at 80°C for 2 h and allowed to cool and equilibrate for 72 h thereafter, with no appreciable change in soil chemistry. Plastic pots (6 × 25 cm) were then filled with 575 g (dry weight) of the steamed soil.

Seed sources

Wheat ancestors

The Wheat Genetics Resource Center (Department of Plant Pathology, Throckmorton Hall, Kansas State University, Manhattan) provided seed of *Triticum carthlicum* (2825), *Triticum persicum* (2811), *T. persicum* (2812), *Triticum pyramidale* (2809), *Triticum polonicum* (2808), *Triticum paleocolchicum* (2807), *Triticum orientale* (2805), *Triticum dicoccum* (1165), *Triticum tauschii* var. *strangulata* (2377, 2452) (syn. *Aegilops squarrosa* var. *strangulata*), *T. tauschii* var. *meyeri* (2529), *T. tauschii* var. *typica* (1649, 1691, 2492), and *A. speltoides* (1773). The USDA, Agricultural Research Service, Department of Agronomy, Throckmorton Hall, Kansas State University, Manhattan, Kans., provided seed of *T. tauschii* var. *typica* (2378, 2448, 2528, 2541, 2567, and 2595) and *T. monococcum* (266844 and 355520).

Modern cultivars

Seed of winter wheat *T. aestivum* cultivars Century, Saluda, Karl, TAM 107, TAM 200, and Wrangler were obtained from the USDA, Agricultural Research Service, Department of Agronomy, Throckmorton Hall, Kansas State University, Manhattan, Kans. Spring wheat cultivars Chinese Spring, Norin 29, Pavon 76, and Spelta were provided by the Wheat Genetics Resource Center.

Seedling treatment

All seed was germinated in 4 × 4 cm plastic pots (four seeds per pot) containing sterile vermiculite. Six days after emergence (2- to 3-leaf stage), seedlings were vernalized in a 4°C growth chamber for 42 days. An 8-h photoperiod was provided by fluorescent lighting. Following vernalization, 10 seedlings of each species were individually transplanted into pots containing steam-pasteurized soil. One-half of the seedlings of each species were inoculated with vesicular–arbuscular mycorrhizal fungal spores at transplant, while the remaining half were not.

Mycorrhizal fungus inoculum preparation

Inoculum for this study was obtained by mixing spores from a variety of species known to colonize wheat (Hetrick *et al.* 1992). *Glomus etunicatum* Becker and Gerd. and *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe were obtained from the Konza Prairie Research Natural Area. Isolates of *Glomus versiforme* (Karsten) Berch and *Glomus intraradix* Schenk and Smith were obtained from Dr. L. Peterson (University of Guelph, Guelph, Ont.). Dr. J. Dodd (University of Kent, Canterbury, Kent, U.K.) provided isolates of *Glomus geosporum* (Nicol. and Gerd.) Walker and *G. mosseae*. These species were mixed and used as inoculum to ensure that incompatibility between inoculant and plant species or cultivars would not affect the results.

TABLE 1. Mycorrhizal growth response, dependence, and root colonization of wheat ancestors

Species and accession no.	Total dry wt. (g)		Growth response (%)	Mycorrhizal dependence (%)	Root colonization (%)
	Mycorrhizal	Nonmycorrhizal			
A genome					
T. monococcum					
PI 266844	1.91	2.01	−5	−5	19.5
PI 355520	1.70	2.00	−15	−18	16.2
S (B and G) genome					
T. speltoides					
1773	1.59	1.49	7	6	14.8
D genome					
T. tauschii var. *typica*					
2492	2.21	1.83	17	21	11.8
1691	1.72	1.81	−5	−5	53.0
1649	1.82	2.05	−11	−13	19.0
2567	2.21	2.00	10	10	13.4
2541	1.80	1.97	−9	−9	16.8
2448	0.51	0.53	1	1	6.0
2378	2.04	2.19	−7	−7	28.0
2420	1.44*	0.53	172	63	17.0
2495	1.14	1.05	9	8	15.8
2528	1.07	0.85	26	21	15.8
T. tauschii var. *meyeri*					
2529	2.67*	1.77	51	34	21.2
T. tauschii var. *strangulata*					
2377	2.40*	1.87	28	22	9.8
2452	2.35*	1.53	54	35	10.2
AB genome					
T. carthlicum					
2825	2.14	2.42	−12	−13	41.8
T. polonicum					
2808	2.16	2.15	0	0	52.8
T. dicoccum					
1165	1.88	2.51	−25	−34	33.6
T. persicum var. *stramineum*					
2811	2.49	2.52	−1	−1	24.4
T. persicum var. *fuliginosum*					
2812	1.88	2.48	−24	−32	23.8
T. pyramidale					
2809	1.84	2.09	−12	−14	13.6
T. orientale					
2805	1.31	1.44	−9	−10	15.2
T. paleocolchicum					
2807	1.88	1.98	−5	−5	13.2

*Mean dry weight of mycorrhizal plant significantly ($P < 0.05$) exceeded nonmycorrhizal counterpart.

Each fungal isolate was propagated individually on asparagus (*Asparagus officinalis* L. cv. UC72) for 18−24 months prior to use. Spores were isolated from pot cultures by wet sieving, decanting, and sucrose density gradient centrifugation (Daniels and Skipper 1982). Spores were suspended in distilled water and combined to obtain a final spore suspension of 400 spores/mL, with approximately 70 spores of each of the six species. One millilitre of spore suspension was pipetted onto roots of seedlings at transplant.

Experimental design and maintenance

Pots were arranged in a randomized complete block design with five replications per treatment. The plants were maintained in a 12−17°C greenhouse for 6 weeks, and subsequently maintained at 20−25°C for the remainder of the study. This variation in greenhouse temperatures was intended to more accurately simulate field conditions. Plants were watered and fertilized every other week with 0.0625 g Peter's No-Phos Special Fertilizer solution (25:0:25, N−P−K; Robert B. Peter Co., Inc., Allentown, Penn.) dissolved in 50 mL water. Thus, approximately 35 $mg \cdot kg^{-1}$ N and $30 \cdot kg^{-1}$ K were added every other week to each pot. After 14 weeks, plants were harvested and shoot, root, and total dry weights were recorded. Subsamples of dried roots were stained in trypan blue (Phillips and Hayman 1970) and examined microscopically to assess percent root colonization using a Petri dish scored in 1-mm squares (Daniels *et al.* 1981).

Statistical analysis

A one-way analysis of variance (ANOVA, $P < 0.05$) was performed on shoot, root, and total dry weights, root colonization, and root to shoot ratio for each plant species using the SAS statistical package (SAS Institute Inc. 1988). Since shoot and root dry weight were each highly correlated with total weight, only total dry weights are presented to simplify data presentation. No obvious trends were observed in the root to shoot ratio data, and thus these data are not presented. Growth responses were calculated for each plant species as follows: percent growth response = [(dry weight inoculated − dry weight

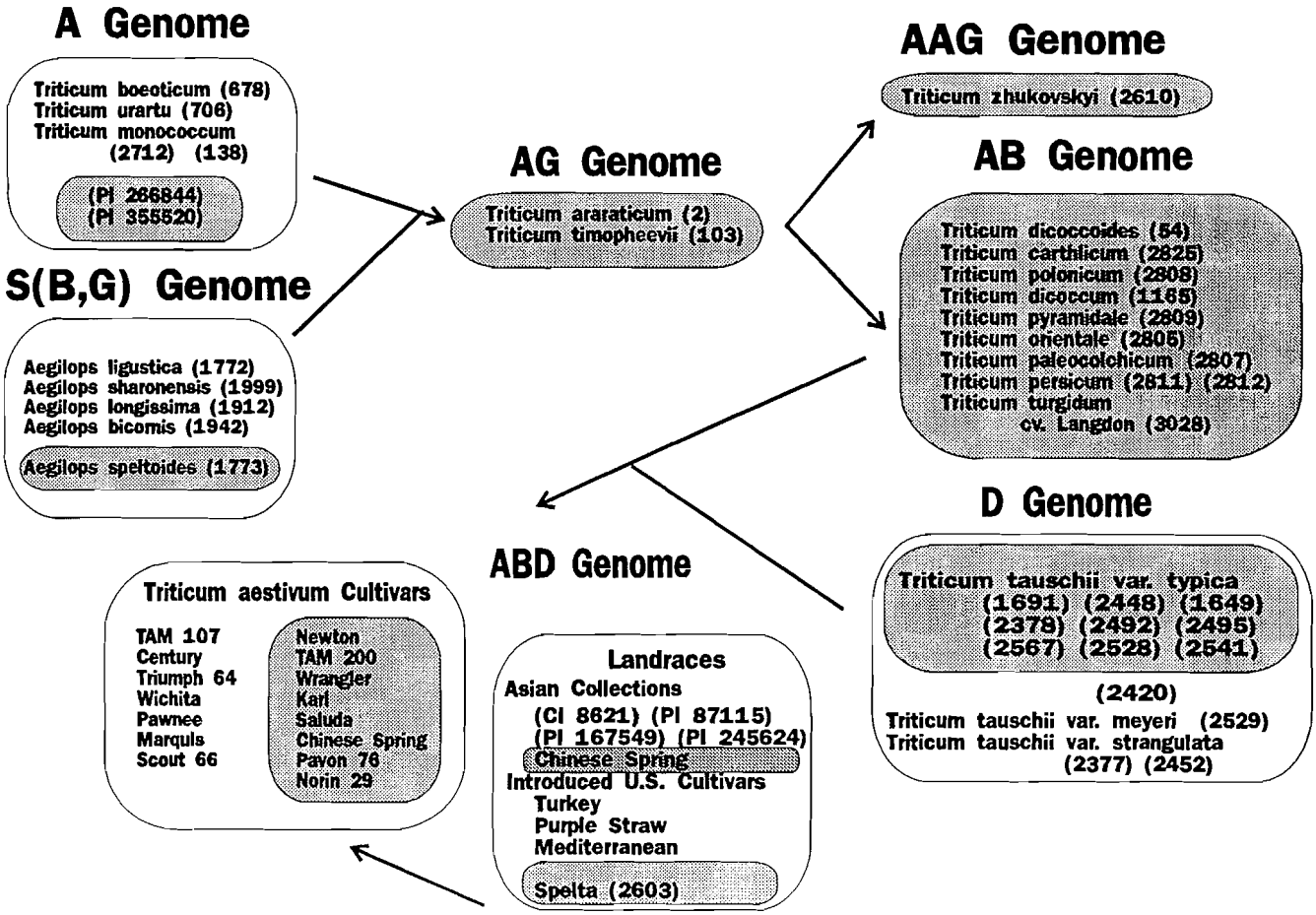

FIG. 1. Schematic diagram detailing the evolution of hexaploid wheat and the responses of various accessions of wheat ancestors to mycorrhizae. Biomass of ancestors or accession numbers in shaded boxes was not significantly improved by inoculation with mycorrhizal fungi.

noninoculated)/dry weight noninoculated] × 100. Mycorrhizal dependence was calculated similarly except the denominator was the dry weight of inoculated rather than noninoculated plants.

Results and discussion

Wheat ancestors

Unlike other *T. monococcum* accessions (A genome) tested previously (Hetrick *et al.* 1992), neither of the accessions tested in the present study displayed dependence on mycorrhizal symbiosis (Table 1). As in the previous study, the *T. speltoides* ancestor was not dependent on the symbiosis. Like the AB genome contributors studied previously, all eight of the ancestors tested in the present study lacked dependence on mycorrhizal symbiosis. Of the nine accessions of *T. tauschii* var. *typica* tested, only one (2420) was dependent on mycorrhizal symbiosis. Both 1691 and 1649 had been tested in the previous study with similar results. In contrast, both *T. tauschii* var. *meyeri* (2529) and *T. tauschii* var. *strangulata* (2377 and 2452) displayed significant dependence on the symbiosis. The latter results are consistent with those of Kapulnik and Kushnir (1991) who observed significant growth responses in an accession of *T. tauschii* var. *meyeri, T. tauschii* var. *strangulata*, and *T. tauschii* var. *typica*. Unfortunately, it is difficult to make any more specific comparisons between ancestors used in the present studies and those studied by Kapulnik and Kushnir (1991) because the selections used in the latter studies cannot be cross-referenced with those catalogued in and maintained by the Wheat Genetics Resource Center. Regardless of response to mycorrhizal symbiosis, roots of all ancestors were colonized (6.0−53.0%) by the fungal symbionts. There was no significant relationship between growth response ($r = -0.159$, $P = 0.557$) or mycorrhizal dependence ($r = -0.264$, $P = 0.323$) and root colonization.

Wheat cultivars

Of the five spring wheat cultivars tested in the present study, only one was significantly affected by mycorrhizal inoculation (Table 2). Biomass of 'Pavon 76' was greater in the absence of mycorrhizae than when inoculated. In contrast, dry weight of two of the five winter wheat cultivars (TAM 107 and Century) was greater when mycorrhizal than nonmycorrhizal. The other three cultivars were not affected by mycorrhizal symbiosis. All wheat cultivars were colonized by mycorrhizal fungus symbionts (9.4−31.6%), but there was no significant relationship between growth response ($r = 0.543$, $P = 0.105$) or mycorrhizal dependence ($r = 0.342$, $P = 0.334$) and root colonization.

Synthesis

By combining the responses of ancestors tested previously (Hetrick *et al.* 1992) with those revealed in the present studies (Fig. 1), some interesting trends become apparent. Although many diploid A- and S-genome ancestors are dependent on

TABLE 2. Mycorrhizal growth response, dependence, and root colonization of spring and winter hexaploid wheat cultivars

Cultivar	Total dry weight (g)		Growth response (%)	Mycorrhizal dependence (%)	Root colonization (%)
	Mycorrhizal	Nonmycorrhizal			
ABD genome					
Spring wheats					
Chinese Spring (3008)	1.83	1.68	9	8	15.0
Spelta (2603)	2.44	2.52	−3	−33	17.2
Pavon 76 (2980)	1.63	2.43*	−33	−49	22.0
Norin 29 (3025)	2.47	2.29	8	7	18.4
Winter wheats					
TAM 107	2.38*	1.60	48	33	31.4
TAM 200	1.95	1.57	24	20	12.8
Saluda	2.46	3.04	−19	−24	11.6
Century	2.29*	1.64	40	28	21.4
Wrangler	2.22	2.43	−8	−9	11.4
Karl	2.25	2.60	−13	−15	9.4

*Mean dry weight of mycorrhizal or nonmycorrhizal plant significantly ($P < 0.05$) exceeded that of mycorrhizal or nonmycorrhizal counterpart.

TABLE 3. Influence of cultivar age on growth response and root colonization of landraces and cultivars of wheat to mycorrhizae

Origin and cultivar	Growth increase (%)	Root colonization (%)
Before 1900		
Asian collections		
PI 167549	334	63.0
PI 245624	158	67.8
CI 8621	133	70.8
PI 87115	49	71.0
Chinese Spring*	9	15.0
Introduced United States cultivars		
Turkey	68	31.1
Purple Straw	67	6.3
Mediterranean	29	20.4
Spelta*	3	17.2
Before 1950		
United States		
Wichita	100	24.4
Marquis	60	18.2
Pawnee	29	45.0
After 1950		
United States		
Scout 66	73	24.6
Triumph 64	51	29.2
Tam 107 (1984)	48	31.4
Century (1986)	40	21.4
Tam 200 (1987)*	24	12.8
Newton (1977)*	14	12.6
Karl (1988)*	13	9.4
Wrangler (1984)*	8	11.4

*Growth was not significantly improved by inoculation with mycorrhizal fungi.

mycorrhizal symbiosis, some accessions of *T. monococcum* (PI 266844 and PI 355520) and *A. speltoides* (1773) lack mycorrhizal dependence. Kapulnik and Kushnir (1991) reported an *A. speltoides* isolate that was stimulated by mycorrhizal symbiosis as well as a *Triticum boeoticum* line that lacked dependence. The existence of both dependent and nondependent A- and S-genome ancestors could explain the lack of response to mycorrhizae apparent in the tetraploid ancestors of the AG and AB genomes we tested as well as the dependence reported by Kapulnik and Kushnir (1991) in the AG-genome ancestor *T. araraticum*. All tests (both those of Kapulnik and Kushnir 1991 and from our laboratory) of AB-genome ancestors are consistent. No evidence of mycorrhizal dependence was observed in these ancestors. For the D-genome ancestor *T. tauschii* var. *typica*, 90% of the lines tested were not dependent on mycorrhizae. However, one accession did display a growth response to mycorrhizae, and one line tested by Kapulnik and Kushnir (1991) was also dependent. In contrast, all accessions of *T. tauschii* var. *meyeri* and *T. tauschii* var. *strangulata* tested in our laboratory and the lines tested by Kapulnik and Kushnir (1991) were dependent on mycorrhizal symbiosis.

Although Kapulnik and Kushnir (1991) observed no dependence on mycorrhizae in the hexaploid wheat cultivars (ABD genome) they tested, 46% (7 out of 15) of the cultivars we have tested in the present study or previously were dependent on the symbiosis. Since *T. tauschii* var. *strangulata* is the D-genome contributor to hexaploid (ABD genome) wheat and was dependent on mycorrhizal symbiosis in the present studies and in the tests conducted by Kapulnik and Kushnir (1991), it appears that mycorrhizal dependence in hexaploid wheats probably comes from the D genome. This contention is supported by the consistent lack of dependence in the AB- and AG-genome ancestors in the lineage of hexaploid wheats.

The lack of mycorrhizal dependence in the four spring wheats tested is surprising. Since 'Chinese Spring' wheat is a relatively old wheat, the lack of mycorrhizal dependence in spring wheats is probably not attributable to losses in mycorrhizal dependence associated with modern breeding practices. Low levels of mycorrhizal dependence in winter wheats have been attributed to its fall-sown habit (Asai 1934) and low soil temperatures, which limit fungal metabolism (Hetrick *et al.* 1984). In contrast, spring-sown crops are usually colonized by mycorrhizal fungi and are generally believed to benefit from mycorrhizae (Hayman 1987).

In our earlier study (Hetrick *et al.* 1992), we observed a strong trend for greater dependence on mycorrhizae in older wheat cultivars and landraces. When those data are combined with the present data, it appears that mycorrhizal dependence in winter wheat cultivars was strong and fairly consistent prior to 1950 (Table 3). It is only in relatively recent releases that mycorrhizal response has become more variable. Presumably, this reflects modern breeding under highly fertile conditions.

A growing body of evidence suggests that the ability to participate in mycorrhizal symbiosis is a heritable trait in plants. The degree of root colonization, number of spores developing from a plant, and alkaline and acid phosphatase activity in roots may differ among cultivars or genotypes (Azcon and Ocampo 1981; Krishna *et al.* 1985; Lackie *et al.* 1988; Kesava Rao *et al.* 1990). Recently, Duc *et al.* (1989) observed that mycorrhiza-resistant mutants could be identified in legumes that also lacked the ability to nodulate (Duc *et al.* 1989). These *myc*$^-$ mutants were not able to be colonized by mycorrhizal fungi, suggesting that the ability of mycorrhizal fungi to infect host plants is a heritable trait in plants. For plants infected by mycorrhizae, however, mycorrhizal dependence or the degree to which the plant will benefit from the symbiosis has been related to host plant characteristics such as root weight (Azcon and Ocampo 1981), P concentration and sugar content of roots (Ratnayake *et al.* 1978), and P content of soil (Lackie *et al.* 1988). That the ability of host plants to benefit from mycorrhizal symbiosis is itself a heritable trait separate and distinct from inheritance of ability to form mycorrhizae has not been previously suggested. Further research will be necessary to confirm this hypothesis and to determine whether mycorrhizal dependence is a multigenically inherited or a more simply inherited trait.

Whereas Kesava Rao *et al.* (1990) observed a positive correlation between the ability of a mycorrhizal fungus to infect roots and mycorrhizal dependence in plant cultivars, no such relationship was observed in wheat by Azcon and Ocampo (1981). Similarly, in the present study and in the previous study (Hetrick *et al.* 1992), no relationship was observed between degree of root colonization and degree of growth benefit from the symbiosis. Thus, although root colonization is obviously a necessary precursor to plant benefit from the symbiosis, in wheat the degree of benefit is not directly related to the degree of colonization. This suggests that different genes may be involved in the colonization process than are involved with nutrient acquisition and translocation to plants.

The ramifications of having genes that foster root colonization in the absence of genes for mycorrhizal dependence are of considerable importance. Growth depressions in response to mycorrhizal symbiosis were described in field-grown tobacco (Modjo and Hendrix 1986). In the previous study of Hetrick *et al.* (1992), each of 10 fungal isolates was inoculated onto three wheat cultivars. All of the isolates colonized 'Turkey' wheat, a mycorrhiza-dependent cultivar, and 8 out of the 10 stimulated biomass production by this cultivar. In contrast, two cultivars lacking mycorrhizal dependence were also colonized by all 10 fungal isolates, but none of the fungal isolates stimulated plant growth, and instead, 30 and 40% of these fungal isolates significantly decreased the dry weight of their hosts (Hetrick *et al.* 1992). Thus, the absence of mycorrhizal dependence may result in pathogenesis. The conditions under which growth depressions are realized in nondependent host cultivars are not yet clear. However, given the lower frequency of mycorrhizal dependence in modern releases and the potential for pathogenesis, the mycorrhizal dependence status of wheat cultivars may be an important consideration. These data suggest that mycorrhizal dependence must be considered not only in breeding programs for low-input agriculture where the nutrient-absorbing capability of the symbiosis is desirable, but also to ensure that the absence of mycorrhizal dependence from host genetic makeup does not result in growth or yield depressions.

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