lunar signals. Ongoing tree-ring collections should eventually provide more suitable data for testing for a spatially nonstationary drought rhythm in the Great Plains and for testing complex hypotheses of solar or lunar-tidal influence on drought.

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Competition for Phosphorus: Differential Uptake from Dual-Isotope–Labeled Soil Interspaces Between Shrub and Grass

Abstract. *Two species of* Agropyron *grass differed strikingly in their capacity to compete for phosphate in soil interspaces shared with a common competitor, the sagebrush* Artemisia tridentata. *Of the total phosphorus-32 and -33 absorbed by* Artemisia, *86 percent was from the interspace shared with* Agropyron spicatum *and only 14 percent from that shared with* Agropyron desertorum. *Actively absorbing mycorrhizal roots of* Agropyron *and* Artemisia *were present in both interspaces, where competition for the labeled phosphate occurred. The results have important implications about the way in which plants compete for resources below ground in both natural plant communities and agricultural intercropping systems.*

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The natural distribution of species is molded to a large extent by interspecific competition. Yet the nature of competition is known more by its manifestations than by its mechanisms. Competition among plants is normally inferred from their performance in experiments in which the competitive setting is manipulated in various ways. These changes include removing or adding neighbors, partitioning the roots or shoots of neighboring plants, or changing resource levels, as by fertilization (*1*). Apart from studies of competition for light or space above ground, it has seldom been possible to observe the manner in which plants compete. Sometimes mechanisms can be inferred from the physiological performance of individual plants tested in isolation (*2*), but it is difficult to make such inferences when plants are growing competitively in a field setting.

We report here a demonstration of differential competitiveness for a specific belowground resource, phosphate, when the actively absorbing roots of different species were intermingled. Experiments were conducted in field plots where sagebrush, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, was growing with two species of *Agropyron* bunchgrass. In this environment *Agropyron desertorum* (Fisch. ex Link) Schult. was much more effective in competing with *Artemisia* than was *Agropyron spicatum* (Pursh) Scribn. and Smith (*3*).

The field plots used had been established 6 years earlier as an evenly spaced matrix of transplanted shrubs and grasses. Each *Artemisia* shrub was surrounded by four grasses, with two of each *Agropyron* species on opposite sides. In these plots there was no overlap of the canopies, but the root systems of the grasses and shrubs were thoroughly intermingled (*4*). For the plant sets chosen, the grasses were similar in size.

Unlike nitrate and many other more diffusible soil nutrient ions, phosphate is almost immobile in soils and is accessible only when it is within a few millimeters of a root (*5*). The effective uptake zone of a root can be extended by root hairs and mycorrhizae, but competition for phosphate among roots can take place only when roots and their associated mycorrhizae are in close proximity (*5*).

To determine how effectively the shrub acquired phosphorous from soil space shared with each of its *Agropyron* neighbors, a dual-isotope technique was used (*6*). The isotopes ^{32}P and ^{33}P were injected separately into soil interspaces on opposite sides of the shrub and halfway between the shrub and each grass species (*7*). Because phosphate ions are quickly bound in these calcareous soils, they do not move appreciably by leaching or diffusion (*8*). Growing shoot tips of the *Artemisia* shrub were then sampled four times over a 56-day period (*9*). The $^{32}P/^{33}P$ ratio technique obviated the need to determine phosphorus isotope pools in the entire plants, which would have been nearly impossible because of the diffuseness of the root systems. The radioisotopes were virtually carrier-free, and the concentrations of the added phosphorus were below those levels shown to influence root or mycorrhizal growth (*7*). The two *Agropyron* grass species have very similar phenological patterns (*4*) and were in the same stage of their seasonal growing patterns.

A large stochastic element was expected, since individual roots would be contacted in the process of injecting the label. Root growth into the radioactive phosphate would also have had a random component. The results, however, were striking in their consistency among the replicate plant sets and over time. All eight replicate sets showed predominant uptake by the shrub on the *A. spicatum* side (Fig. 1A). There was a similar pattern of change in the rate of radioactive phosphate appearance in the shoots of *Artemisia* for isotopes absorbed from the two sides of the shrub. Thus the average ratio of isotope acquisition from the two sides remained about the same during the experiment (Fig. 1A). Over the 56 days, *Artemisia* obtained 86 percent of the total radioactive phosphorus from the interspace shared with *A. spicatum*.

To determine whether the rooting density (length of root per unit of soil volume) differed on the two sides of *Artemisia*, we sampled nonradioactive replicate plant sets by soil auger (*10*). Rooting densities of the shrub did not differ statistically between the interspaces (Fig. 1B).

The presence and condition of mycorrhizae were also assessed because they play an important role in facilitating phosphorus uptake. Vesicular-arbuscular mycorrhizae of the genus *Glomus* were present on the roots of all three species. The frequency of mycorrhizal infection in both its vesicular and arbuscular forms did not differ statistically between the two sides of the shrub (Table 1) (*11*). There was also no statistically significant difference in the rate of infection of *Artemisia*, gauged as the number of fungal penetrations per centimeter of root with established mycorrhizae in which arbuscules were present (Table 1). (Arbuscules are considered to be the active transfer organ of the fungus.) Mycorrhizal spores in the interspace soil were abundant on both sides of *Artemisia* (*11*).

The presence of mycorrhizal *Artemisia* roots in equal quantities and similar condition in both interspaces and of abundant spores for initiating new infection indicate that there should have been no difference in the capacity of the roots to absorb phosphorus. Inhibition of *Artemisia* roots in the presence of *A. desertorum* roots cannot be excluded but appears unlikely. It is also possible that phosphorus was transferred from *A. spicatum* to *Artemisia* after it had already been absorbed by the grass. Transfer phenomena have been reported, but the net quantities of phosphorus transferred are not likely to be significant (*12*). Even if interference or a significant transfer of phosphorus had taken place, the net result is still that *Artemisia* absorbed more phosphorus when sharing space with *A. spicatum* than with *A. desertorum*.

The radioisotope content of the grasses was consistent with the differential uptake by *Artemisia*. At the end of the experiment we determined the total phosphorous isotope content of the entire shoot of each of the grasses. *Agropyron desertorum* contained nearly four times as much isotope as did *Agropyron spicatum* (Table 2). Assessment of total isotope quantities in crowns and roots was not feasible, but concentrations in samples from the roots were also significantly higher in *A. desertorum* (Table 2). The potential for *A. desertorum* to absorb more phosphorus than *A. spicatum* is suggested by the greater number of fungal infection units (Table 1).

We do not wish to imply that phosphorus is the single pivotal resource in the balance of competition. Indirect evidence, for example, shows that *A. desertorum* is more effective than *A. spicatum* in rapidly extracting moisture when competing with *Artemisia* (*13*). These resources are complementary in that more effective moisture uptake facilitates absorption of phosphorus, and better phosphorus nutrition facilitates the capacity of plants to acquire water (*4*, *14*).

In summary, *Artemisia* obtained much less phosphorus from soil space shared with *A. desertorum* than from space

Table 1. Vesicular-arbuscular mycorrhizae associated with roots of *Artemisia* and the *Agropyron* grasses in interspaces. Different superscript letters within a column indicate values that differ significantly ($P < 0.05$, one-way analysis of variance followed by 2 × 2 comparisons). Data were first subjected to an arc-sine transformation.

Species	*n*	Percentage of root length		Number of penetrations per centimeter of root with arbuscules
		With arbuscules	With vesicles	
Artemisia (*Agropyron spicatum* side)	4	49[a]	60[a]	16[a]
Artemisia (*Agropyron desertorum* side)	4	43[a]	61[a]	16[a]
Agropyron spicatum	4	63[b]	52[b]	9[b]
Agropyron desertorum	4	72[b]	48[b]	19[a]

Table 2. Concentrations of radioactive phosphorus in samples from shoot, crown, and root tissues and total quantity in shoots (median values). Root and shoot concentrations and quantities are significantly different between species ($P < 0.05$, Wilcoxon rank-sum test; $n = 8$). Crown concentrations are not significantly different.

Species	Concentration (cpm/g)			Total content in shoots (count/min per plant)
	Shoots	Roots	Crowns	
A. spicatum	3.86×10^3	1.80×10^3	2.52×10^3	1.50×10^5
A. desertorum	2.56×10^4	6.29×10^3	4.52×10^3	5.79×10^5

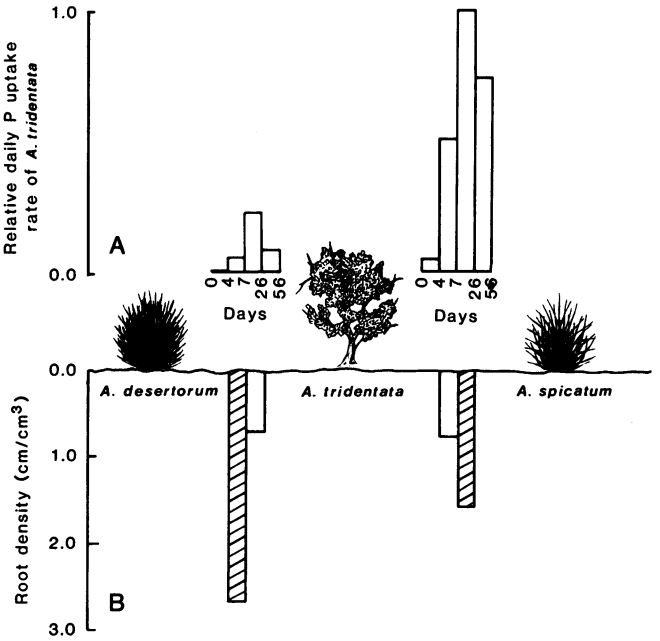

Fig. 1. (A) Relative rate of phosphorus absorption—that is, average daily uptake of isotopes by shoot tips of *Artemisia* from soil interspaces shared with *A. spicatum* and *A. desertorum* at various times after labeling. The values are averages of eight replicate plant sets, all of which showed predominant uptake by the shrub on the *A. spicatum* side. The proportion of total isotope in the shoots that was obtained from the *A. spicatum* side during the period from labeling to days 4, 7, 26, and 56 was 97 percent (95 percent confidence interval, 84 to 100 percent), 92 percent (79 to 99 percent), 84 percent (74 to 92 percent), and 86 percent (76 to 94 percent), respectively (data analyzed following arc-sine transformation). (B) Rooting densities (*15*) of the grasses (crosshatched bars) and *Artemisia* (open bars) in the interspaces where the isotopes were placed. Four replicate sets of plants were sampled for rooting density. The grass rooting density was significantly greater than the shrub rooting density ($P = 0.043$), but neither the shrub nor the grass rooting density differed significantly between the two sides of the shrub.

shared with *A. spicatum*. This striking difference in phosphorus acquisition occurred in zones where there was an abundance of actively absorbing roots of both shrub and grass. These results indicate that *A. desertorum* has a great capacity to obtain phosphate at the expense of *Artemisia*, even though the shrub has invested as much in root length and mycorrhizal associations in the interspaces with *A. desertorum* as in the interspaces shared with *A. spicatum*. This provides evidence of competitive exploitation as a mechanism of interspecific competition.

These findings also have implications for agricultural intercropping systems. Analogous experiments could provide important information on the competitiveness of different crop species for phosphate and the effectiveness of phosphate fertilization patterns.

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8. The concentration of exchangeable phosphorus in these soils is <6 ppm. Phosphorus desorption tests indicate 90 to 95 percent of added phosphorus is bound to these soils.
9. The length of the experiment was limited by the short half-lives of the isotopes. The counts of the two isotopes were corrected for half-life, counting efficiency, and overlap of energies.
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The Crystallization of Ultralong Normal Paraffins: The Onset of Chain Folding

Abstract. *The nature of chain folding in polymers and the determination of the chain length at which folding occurs have been central questions in polymer science. The study of the formation of lamellar polymer crystals through chain folding has received a new impetus as a result of the recent synthesis of normal alkanes of strictly uniform chain lengths up to C_{390} H_{782}. Chain folding is found in all such paraffins starting with $C_{150}H_{302}$. As with polyethylenes obtained by conventional polymerization, the fold length in the normal alkanes varies with crystallization temperature, but it is always an integral reciprocal of the full chain length. This behavior indicates that the methyl end groups are located at the lamellar surface and that the fold itself must be sharp and adjacently reentrant.*

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One of the most remarkable characteristics of flexible polymers is that they crystallize by chain folding (*1*). There are still many questions about this general, yet largely unexplained, phenomenon and also controversial problems (*2*). Possibly one of the most intriguing questions concerns the transition from the traditional behavior of short-chain molecules to that of a typical polymer. More specifically, at what chain length does chain folding set in and what is the nature of this fold?

It is evident that the primary prerequisite for such an inquiry is the strict uniformity of the chain length in the material to be examined. Further, the chains must have end groups that are not "alien" to the system. Moreover, there should be sufficient background information on the crystallization behavior of the material, both in the oligomeric state and in the polymeric state. In past experiments (*3–9*), these conditions were never all satisfied simultaneously. As a consequence, conclusions such as could be reached were not sufficiently definitive or general to constitute a representative solution of the central problem.

Normal alkanes (*n*-alkanes) the oligomers of polyethylene, would be the best materials to examine, provided that sufficiently uniform preparations could be obtained with increasing chain lengths of up to several hundred carbon atoms. As a result of a new synthesis (*10, 11*), such materials have become available. The maximum length reached so far is $C_{390}H_{782}$, which should ensure overlap with polyethylenes obtained by conventional polymerization where chain folding is consistently observed.

We now report that *n*-alkanes with lengths as short as $C_{150}H_{302}$ are capable of crystallizing in a chain-folded manner. The fold lengths are integral reciprocals of the total chain lengths, and thus the chain ends must lie at the layer surfaces. The fold itself cannot contain more than a few chain members; hence it must be sharp and adjacently reentrant.

The *n*-alkanes used were prepared by the method of Bidd and Whiting (*11*) and had the following extended-chain melting points (T_m) as determined by differential scanning colorimetry (DSC) to an accuracy of 0.3 K: $C_{102}H_{206}$, T_m = 388.9 K; $C_{150}H_{302}$, T_m = 396.4 K; $C_{198}H_{398}$, T_m = 399.8 K; $C_{246}H_{494}$, T_m = 401.8 K; $C_{294}H_{590}$ (*12*), T_m = 403.6 K; and $C_{390}H_{782}$, T_m = 405.2 K. A comparison of T_m for our $C_{150}H_{302}$ with the data reported for the longest *n*-alkanes prepared in the past [394.2 K for $C_{140}H_{282}$ (*13*) and 395.4 K for $C_{160}H_{322}$ (*14*)] indicates a clear improvement in purity in our materials.

The samples were crystallized both from the melt and from solutions (Table