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Competitive Effects of Various Grasses and Forbs on Ponderosa Pine Seedlings

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ABSTRACT. Competition between ponderosa pine seedlings and various grasses and forbs was studied on a site in northern Arizona burned in 1982 by a wildfire. Two-year-old pine seedlings were planted in 3.05 × 3.05 m plots in April 1983, followed by the sowing of grass and forb seeds on the same plots in July 1983 after summer rains had begun. Predawn xylem water potential of the pine seedlings was measured biweekly throughout the 1983 and 1984 growing seasons. Extractable soil nitrogen was measured at the beginning and end of both growing seasons. After the wildfire, nitrate and ammonium levels were significantly higher in the burned area than in an adjacent unburned area. Nitrate and ammonium concentrations in various grass treatment plots were significantly ($P < 0.05$) different at both the beginning and end of the growing season. Pine seedling xylem water potential differed among treatments, with potentials being lowest on plots sown with *Agropyron desertorum*. The differences in seedling xylem water potential and available soil nitrogen were reflected in differences in pine seedling growth. The most effective competitors were *Agropyron desertorum* and *Dactylis glomerata*. Results indicated that competition occurred for both moisture and available nitrogen. FOR. SCI. 33(2):356–366.

ADDITIONAL KEY WORDS. Competition, xylem water potential, nitrate, ammonium, *Pinus ponderosa*.

REGENERATION OF SEVERELY BURNED ponderosa pine (*Pinus ponderosa* Laws.) stands is an expanding problem for resource managers in the Southwest because of the increased frequency of large wildfires (J. S. Barrows, unpublished data).[1] Part of the forest regeneration problem is attributable to competition for water from grasses sown on the burned sites (Pearson 1942, Larson and Schubert 1969). Ponderosa pine growth is also limited on many sites by a lack of available soil nitrogen (Heidmann et al. 1979, Cochran 1979, Powers 1980).

One objective of this study was to determine how different herbaceous species affect survival and growth of ponderosa pine seedlings. Previous work (Baron 1962, Larson and Schubert 1969) indicated that various plant species differentially influenced ponderosa pine seedling growth and mortality, but these studies did not include many species frequently sown on

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[1] Barrows, Jack S. 1978. Lightning fires in southwestern forests. Final report prepared by Colorado State University for Intermountain Forest and Range Experiment Station under Cooperative Agreement 16-568-CA with Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

wildfire sites in the Southwest. A second objective was to investigate whether various herbaceous species had different effects on pine seedling xylem water potential, soil moisture, and soil nitrogen levels.

Methods

Site Description

The study site was located approximately 40 km north of Flagstaff, Arizona, latitude 35°27′, longitude 111°45′, at an elevation of 2290 m. Precipitation at the Fort Valley Experimental Station, which is the closest gaging station (30 km south of the study site), normally exceeds 50 cm per year. Typically there is a drought in May and June when average precipitation is only 1.75 cm and 1.93 cm, respectively (Schubert 1974). Mean monthly temperatures range from about 16°C in the summer to −2°C in the winter and the average frost-free growing season is 94 days (Avery et al. 1976). Soils in the area are derived from basalt and cinder parent material. They are classified as Bandera clay loam, a cindery Torriorthentic Haploboroll (Miller and James 1972).

The 19.4 ha area was burned by a wildfire in June 1982. The fire was intense, eliminating virtually all plant species and the forest floor layer. Standing dead trees were left with the exception of larger trees (>30.5 cm dbh), which were removed in a salvage logging operation.

The study area is within a ponderosa pine-bunchgrass community composed of pole-sized overstory trees and an understory of squirreltail (*Sitanion hystrix* [Nutt.] J. G. Smith), mountain muhly (*Muhlenbergia montana* [Nutt.] Hitch.), Arizona fescue (*Festuca arizonica* Vasey), lupine (*Lupinus* spp.), and others. The pine stand had been thinned approximately three years prior to the fire and the thinning slash had been scattered over the area.

Study Design

A 35.05 m by 35.05 m area within the burn was selected on the basis of its homogeneous overstory prior to the wildfire, uniformity of fire behavior (all trees had almost complete needle consumption, and mortality was 100%), and uniformity of soil conditions. Within this area, 100 3.05 m by 3.05 m plots were established in a square grid. After removing dead stems that were lying on the ground, each plot was planted in April 1983 with nine 2-year-old pine seedlings spaced approximately 0.76 m apart. Seedlings were provided by the USDA Forest Service and were grown from seed collected in the Long Valley area, about 64 km southeast of Flagstaff, Arizona. The Forest Service had determined that this seed source would provide seedlings best suited to the study area. Because of extended drought conditions the first summer, each seedling was watered by hand twice in June to reduce mortality. No other supplemental watering occurred.

Six potential competitors of ponderosa pine seedlings were chosen for this study, including four grasses and two forbs. The grasses included: (1) *Bouteloua gracilis* (H.B.K.) Lag ex Steud. (blue grama), (2) *Dactylis glomerata* L. (orchardgrass), (3) *Sitanion hystrix* (Nutt.) J. G. Smith (squirreltail), and (4) *Agropyron desertorum* (Fisch.) Schult. (crested wheatgrass). *Melilotus officinalis* (L.) Lam. (yellow sweet clover) and *Sanguisorba minor* Scop. (small burnet) were the forbs. All of these species were chosen because they provide forage for wildlife and livestock or are considered good for erosion control.

Twelve plots were randomly chosen for each treatment and were weeded

periodically to remove any species other than those assigned to that plot. Ten plots were randomly chosen as natural competition plots, which were allowed to develop naturally with whatever postfire species became established. Twelve plots were randomly chosen as control (denuded) plots, which were periodically weeded to remove all competing vegetation. The remaining four plots were eliminated prior to the above selections because they had characteristics atypical of the site, such as soil surface depressions caused by the burning of large stumps. Seeding of competing species occurred in July 1983, after the summer rains had started.

The entire study area was enclosed by a 1.83 m high, 2.54 cm mesh inner fence and a 4-strand barbed wire outer fence. The fences excluded elk, deer, livestock, and smaller, nonburrowing mammals from the plots.

Growth Measurements

Diameter 2 cm above the root collar and height of each seedling were measured immediately after planting and again at the end of the second growing season (October 1984). Plots were also checked biweekly to monitor mortality of the seedlings.

Xylem Water Potential Measurements

Predawn xylem water potential was measured biweekly on pine seedling fascicles with a pressure chamber (Scholander et al. 1965). Fascicles were used so that several measurements could be made on a single seedling over the two year period of this study (two 5-month growing seasons). The use of pine fascicles for water stress measurements was assessed by several authors (Waring and Cleary 1967, Johnson and Nielson 1969, Cleary 1970, Hinckley et al. 1978) and shown to be comparable to twig measurements.

To follow seasonal trends in water stress, pine seedlings were selected randomly from a subset of the control plots for xylem water potential measurements in 1983. This sampling was expanded in 1984 to include natural, *Bouteloua gracilis, Dactylis glomerata,* and *Agropyron desertorum* plots. These plots were not included in 1983 because the seeded competitors did not emerge until late in the growing season. Seedlings in 1984 were chosen randomly with exclusion so that no seedling was measured more than four times in a growing season. This procedure minimized the influence of needle sampling on growth and xylem water potential. Precipitation was monitored throughout the growing season with a recording rain gauge.

Soil Nitrate and Ammonium Measurements

Random soil samples were collected from 0–5 cm and 5–15 cm depths using a 2.5 cm diameter soil sampling tube. Two core composites were taken at each of 20 sample sites on both the burned area and an adjacent unburned area in June 1983, before summer rains began. Soils were sampled again in the same manner only on the burned area in September 1983, after the summer rains, to monitor nitrate and ammonium changes on the burned area. In 1984, soils were sampled in June and September on control, *Bouteloua gracilis,* and *Dactylis glomerata* plots. Since we were unable to do chemical analysis on all treatment plots, these plots were chosen to represent a range of potential competitors.

For ammonium and nitrate analysis, soils were sieved (2 mm) immediately in the field, and a 10–20 g subsample was added to a preweighed 125 ml bottle containing 100 ml of 2 M KCL (acidified with HCL to pH = 2.5). The extractant contained 1 ppm phenyl mercuric acetate as a preservative. The soil weight was determined by a second weighing of the bottle. Soil dry weight was determined from a second sample that was dried in a forced air

oven at 105°C until weight loss ceased (W. W. Covington, personal communication). Ammonium (NH_4-N) and nitrate (NO_3-N) concentrations were determined colorimetrically in the KCL extract using the Technicon AutoAnalyzer (Technicon 1973, 1977).

Statistical Analysis

Differences in height and diameter of ponderosa pine seedlings among treatments at the end of the two-year study were analyzed with analysis of covariance (ANOVA) using weighted averages (Dixon 1983). Covariates for final seedling height were initial seedling height and percent cover of potential competitors on the plot. Covariates for final seedling diameter were initial seedling diameter and percent cover of potential competitors on the plots. Using initial size at time of planting as a covariate separated any effects of initial size on final size from the effects of the treatments (species) themselves. Using percent cover of competitors as a covariate separated any effects of quantity of competitor on seedling size from effects of the species themselves. We attempted to keep density of competitors consistent among species through regulation of seeding rates. However, establishment of plants varied both within and between species. Consequently, we visually estimated percent cover of competitors at the end of the study and used those values as covariates to indirectly remove any effects of density differences among species. Since treatments were applied at the plot level, rather than on individual seedlings, analyses were conducted on plot averages of surviving seedlings to avoid artificially inflating degrees of freedom, a form of pseudoreplication (Hurlbert 1984). Plot averages were weighted by the number of surviving seedlings in each plot, thus giving more importance to plots whose averages were based on more seedlings. When ANCOVA was significant, comparisons of mean growth among treatments were conducted using Duncan's Multiple Range Test on adjusted, weighted values (Hull and Nie 1981). Survival data were transformed by the arc sine function to approximate normality (Zar 1984) and then analyzed by a one-way analysis of variance (Dixon 1983).

Differences in soil ammonium and nitrate between the burned area and an adjacent unburned area, as well as their seasonal changes on the burned site, were analyzed with the nonparametric Mann-Whitney U-test (Dixon 1983). The nonparametric Kruskal-Wallis one-way analysis of variance (Dixon 1983) was used to analyze the differences in xylem water potential, soil ammonium, and soil nitrate among competition treatments in 1984. When the Kruskal-Wallis test was significant, a nonparametric equivalent to Tukey's multiple comparison technique (Zar 1984) was used to determine which treatment means were significantly different. We chose to use nonparametric tests to analyze these data to avoid problems with normality and heterogeneous variances. All tests were conducted at a 0.05 significance level.

Results

Survival and Growth

Ponderosa pine seedling survival did not vary significantly among treatments. Forty percent of the seedlings died during the two-year period of this study. Over half (51%) of the mortality occurred by July 1, 1983, which was before any competitors were seeded on the plots (with the exception of natural plots, which were allowed to seed in naturally). Ninety percent of the mortality occurred by the end of the first growing season, when competitors

had just become established and did not represent much biomass on the plots.

Both the height and diameter growth of ponderosa pine seedlings varied significantly among treatments (Table 1). Seedlings on denuded plots were significantly larger in height and diameter than those on *Sanguisorba minor, Melilotus officinalis, Dactylis glomerata,* and *Agropyron desertorum* plots, but were not significantly different from those on *Bouteloua gracilis* and *Sitanion hystrix* plots (Table 1). The diameter of seedlings on denuded plots was significantly greater than the diameter of those on natural plots, but no difference existed in height. Within the group of species (*A. desertorum, D. glomerata, S. minor,* and *M. officinalis*) that were consistently associated with reduced growth of pine seedlings relative to that under no competition (denuded plots), *Melilotus officinalis* had a significantly smaller effect on pine seedling height and diameter than did *Agropyron desertorum.*

Pine Seedling Moisture Status

Predawn xylem water potential of the pine seedlings varied among treatments throughout the 1984 growing season except on the July 31 sampling period when all water potential measurements were high (Table 2). On May 22, seedlings on *A. desertorum* plots had the lowest mean water potential (−1.05 MPa), which was significantly lower than those on the control (−0.60 MPa) and natural (−0.50 MPa) treatment plots. From June 5 to July 17 seedling water potentials on *A. desertorum* plots were significantly lower than on *B. gracilis* plots. There were no significant differences between these treatments the remainder of the growing season until September 25, when seedling water potentials on *A. desertorum* plots were again significantly lower than on *B. gracilis* plots.

Seedling water potential on control plots was significantly higher than that on *A. desertorum* plots during the early part of the growing season (May 22 to July 17) until the summer rains began. At the end of the growing season (August 29 and September 25), when rainfall events were again less frequent, seedling water potential on control plots was significantly higher than seedlings on *A. desertorum* plots. Seedlings on control plots also had significantly higher water potentials than seedlings on *D. glomerata* plots on September 11 and September 25. Natural vegetation plots had significantly higher pine seedling water potential than *A. desertorum* plots on May 22, June 19, and July 3. Late in the growing season (September 25), pine seed-

TABLE 1. Average height and diameter of ponderosa pine seedlings on treatment plots at the end of the second growing season. Averages are adjusted values based on the overall regression between covariates and height or diameter at the end of the second growing season for seedlings that survived the first two growing seasons.

Species	Height (cm)	Diameter (cm)
Agropyron desertorum	21.8 a[1]	1.0 a
Dactylis glomerata	23.5 ab	1.1 ab
Sanguisorba minor	23.9 ab	1.1 abc
Melilotus officinalis	24.4 b	1.2 bc
Natural	28.4 c	1.3 cd
Sitanion hystrix	28.4 c	1.4 de
Bouteloua gracilis	29.0 c	1.4 e
Control (denuded)	31.0 c	1.4 e

[1] Average values in a column followed by different letters are significantly different ($P < 0.05$) according to Duncan's Multiple Range Test (Nie et al. 1975).

TABLE 2. Ponderosa pine predawn xylem water potential (−MPa) changes with various grass species for the 1984 growing season.

Species	5/22	6/5	6/19	7/3	7/17	7/31	8/14	8/19	9/11	9/25
Bouteloua gracilis	0.67ab[1]	0.39b	0.54b	0.37c	0.31b	0.33a	0.30ab	0.33a	0.35a	0.34bc
Dactylis glomerata	0.65ab	0.69ab	1.32a	1.14ab	0.42ab	0.31a	0.32ab	0.29ab	0.37a	0.47ab
Agropyron desertorum	1.05a	1.11a	1.55a	1.41a	0.56a	0.33a	0.39ab	0.36a	0.39a	0.60a
Control	0.60b	0.44b	0.48b	0.40c	0.36b	0.29a	0.25b	0.22b	0.24b	0.31c
Natural vegetation	0.50b	0.46ab	0.56b	0.61bc	0.42ab	0.28a	0.49a	0.28ab	0.28ab	0.35bc

[1] Average values in a column which are not followed by the same letter are significantly (p 0.05) different according to a nonparametric equivalent to Tukey's multiple comparison technique.

lings in the natural vegetation plots again had significantly lower xylem water potential than seedlings in the control plots.

A. desertorum appears to be the most effective competitor for soil moisture because of its influence on ponderosa pine xylem water potential. Although for most of the 1984 growing season *D. glomerata* did not have an effect statistically different from that of *A. desertorum,* water potentials were always lower on *A. desertorum* plots. *B. gracilis* plots often had higher pine seedling water potential than *A. desertorum,* which suggests that this species is not as good a competitor for soil moisture. *B. gracilis* plots were seldom significantly different in pine seedling water potential from the control plots.

Soil Ammonium and Nitrate

In 1983, nitrate and ammonium concentrations were significantly higher on the burned area than the unburned area at both soil depths (Table 3) except for the level of ammonium at the 5–15 cm soil depth. Ammonium and nitrate levels were significantly reduced after the summer rains at the 0–5 cm soil depth on the burned site (Table 4). However, at the 5–15 cm soil depth there was no significant difference between time periods in nitrate concentration, but there was a significant increase in ammonium concentration after the summer rains. Soil nitrate concentrations at both depths were significantly lower in the *D. glomerata* plots than in *B. gracilis* and denuded plots in June, 1984 (Table 5). However, ammonium concentrations were significantly higher in the *D. glomerata* plots, generally. The same trend was found among treatments for the September 1984 sampling period (Table 5), but the concentrations of ammonium and nitrate were much lower than the June 1984 sampling period. These forms of nitrogen, especially nitrate, are much less abundant at the end of the growing season, probably because of leaching by the summer rains and plant uptake.

Discussion

Seedling Survival, Growth, and Moisture Status

Ponderosa pine seedling mortality was due to transplant shock, poor planting stock, and the spring/early summer drought. Although several studies have shown that seedling mortality is greater when competition is present (See Stewart et al. (1984) for a bibliography with abstracts of such studies), the lack of a competitive effect on mortality in this study was not surprising. Most (90%) of the mortality occurred during the first growing season before competing species had grown much; 51% of the mortality occurred before the competitors had even been seeded. Consequently, factors unrelated to species competition seemed to cause the mortality.

Much of the first season mortality could be attributed to moisture stress. Even though the seedlings were watered twice in June, average seedling

TABLE 3. Extractable soil nitrogen comparisons between burned and unburned areas (June 1983).

	NO_3 – N (ppm)		NH_4 – N (ppm)	
Treatment	0–5 cm	5–15 cm	0–5 cm	5–15 cm
Burned	12.52a[1]	2.00a	6.11a	2.29a
Unburned	0.10b	0.04b	2.82b	2.37a

[1] Column values followed by different letters are significantly different ($P < 0.05$) according to a Mann-Whitney U-test (Dixon 1983).

TABLE 4. Extractable soil nitrogen comparisons between June 1983 (before the summer rains) and September 1983 (after the summer rains) on the burned area.

	NO_3 – N (ppm)		NH_4 – N (ppm)	
Time period	0–5 cm	5–15 cm	0–5 cm	5–15 cm
June 1983	12.52a[1]	2.00a	6.11a	2.29a
Sept. 1983	8.90b	3.56a	2.37b	3.13b

[1] Column values followed by different letters are significantly different ($P < 0.05$) according to a Mann-Whitney U-test (Dixon 1983).

predawn water potentials on control plots in 1983 were lower than −2.0 MPa. Individual seedlings with potentials below −4.0 MPa usually died within two weeks (Elliott, unpublished data). According to Cleary (1970), −2.0 MPa water potential in ponderosa pine seedlings is low enough to result in reduced photosynthesis. In the following year (1984), seedling water potential measurements were much higher on all the treatment plots compared to the first year. However, predawn xylem water potentials were significantly different among competition treatments, which could account for pine seedling growth differences. The growth reduction in height and diameter of pine seedlings on the *D. glomerata* and *A. desertorum* plots compared to those on *B. gracilis* and control (denuded) plots can be related to competition for moisture. Pine seedlings on the *B. gracilis* and control plots had significantly higher xylem water potential (Table 2), especially during the early part of the growing season in 1984. The differences in seedling water potentials between these treatments were greatest during periods of low precipitation and low soil moisture. At times when precipitation was highest, seedling water stress was reduced, even on the highly competitive *A. desertorum* plots. This result suggests that precipitation can alleviate the negative effects of grass species, but the critical elements may be the timing of the precipitation, the duration of the drought period, and the period of growth of potential competitors. If the seedlings are undergoing moisture stress during their early season growth, then lack of water could significantly limit growth. Competition for moisture at this time would magnify growth reduction.

Bouteloua gracilis appears to be a less efficient competitor for soil moisture due in part to its very shallow root system (Kemp and Williams 1980). Also, *B. gracilis* puts on growth later in the growing season and thus does not compete excessively for soil moisture during the early season drought period. Because *B. gracilis* requires less moisture for its growth and devel-

TABLE 5. Extractable soil nitrogen comparisons among control, Bouteloua gracilis, *and* Dactylis glomerata *plots for two time periods (June 1984 and September 1984).*

	June 1984				Sept. 1984			
	NO_3 – N (ppm)		NH_4 – N (ppm)		NO_3 – N (ppm)		NH_4 – N (ppm)	
Treatment	0–5 cm	5–15 cm	0–5 cm	5–15 cm	0–5 cm	5–15 cm	0–5 cm	5–15 cm
Control	17.88[a1]	5.43[a]	2.03[b]	1.48[a]	4.37[a]	3.07[a]	2.14[a]	2.38[a]
Bouteloua gracilis	15.75[a]	3.81[a]	3.66[a]	1.69[a]	1.60[a]	2.68[a]	1.96[a]	2.40[a]
Dactylis glomerata	1.75[b]	.29[b]	3.90[a]	2.52[b]	.18[b]	.12[b]	2.88[b]	3.32[b]

[1] Column values followed by different letters are significantly different at the 0.05 level by a nonparametric equivalent to Tukey's multiple comparison technique (Zar 1984).

opment than *A. desertorum* and *D. glomerata* (Sala et al. 1982), the pine seedlings in these plots underwent less moisture stress.

Although shading could be a factor in the competitive differences among these grass species, root competition for nutrients and moisture is probably the principal factor causing the growth differences found in this study. Barnes (1984) found that *Agropyron trachycaulum* was more efficient at extracting soil moisture from the 20 to 30 cm soil depth than other grasses because of its deep, dense rooting pattern. *Dactylis glomerata* is also a very effective competitor for soil nutrients because of its deep rooting pattern (Remison 1978).

Growth and Nitrogen Availability

Nitrogen in northern temperate forests is often limiting to plant growth because the fraction of soil nitrogen in a readily available form at any one time is rarely more than 1% (Scarsbrook 1965). Ammonium (NH4-N) and nitrate (NO3-N) are the two forms of nitrogen in the soil that are available for plant uptake (Kirkby 1981). Therefore, a primary concern of this study was to determine relative amounts of these ions found in the soil horizons.

As expected, nitrate and ammonium concentrations were much higher on the burned area than the unburned area in June 1983. This phenomenon was probably attributable to increased microbial mineralization associated with higher soil moisture and temperature in burned areas (Lavender and Walker 1979), and to the immediate release of organic nitrogen during burning (Mroz et al. 1980, Debano and others 1979, Raison 1979, Klemmedson 1976). Later in 1983, both nitrate and ammonium concentrations had significantly decreased at 0–5 cm soil depth. However, nitrate levels were not significantly different in the 5–15 cm soil depths between time periods, but ammonium concentrations were significantly higher. These differences found in soil nitrogen between time periods in 1983 and between the two soil depths indicate that much of the nitrate that was found in the 0–5 cm depth after the burn may have been leached into the 5–15 cm depth by precipitation. The decrease in nitrate was not attributed to plant uptake because soil samples were taken from areas denuded of all vegetation. The trend in 1984 was a high initial level of nitrate (June) which decreased at the end of the season (September) similar to the trend in 1983. The low concentration of soil nitrate in the *D. glomerata* plots compared to control and *B. gracilis* plots was probably caused by uptake by Dactylis, which shows substantial early growth. The only time that ammonium levels on the *B. gracilis* plots were significantly different from those on control plots was in June at the 0–5 cm soil depth. Soil nitrate levels were never significantly different between *B. gracilis* plots and denuded plots. While nitrate levels were much lower on *Dactylis glomerata* plots, ammonium concentrations were significantly higher than those found on denuded or *B. gracilis* plots.

This pattern of nitrate and ammonium concentrations was also observed by Welch and Klemmedson (1975), who compared soils from a ponderosa pine ecosystem and an adjacent open grass system of mountain muhly and Arizona fescue. They hypothesized that nitrate was more important in the pine ecosystem and that ammonium was more important in the grass system, because ammonium was the most abundant form of nitrogen in the grass system. However, it is possible that soil ammonium concentration was higher in the grass system because grass species preferentially absorb nitrate. In contrast, the pine plants may primarily utilize the ammonium ion form of nitrogen because they do not have adequate nitrate reductase capacity to assimilate sufficient nitrate (Bigg and Daniel 1978). There could

also be different nitrification rates in these two ecosystems because of temperature and moisture differences or allelopathy. This explanation would hold for the differences we found in this study as well. Pine seedlings may utilize ammonium while *D. glomerata* preferentially absorbs nitrate.

Another mechanism by which grasses could cause growth reduction in ponderosa pine seedlings is allelopathy. Rice (1974, 1979) has suggested that some grass species can inhibit nitrification rates in some systems and also cause direct toxic effects. However, we have no data with which to address this possibility.

In conclusion, species differed significantly in terms of their effects on ponderosa pine seedling growth. Different abilities to compete for moisture and nitrate at times when those resources are most limiting to pine seedling growth may explain differences in species effects.

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