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BRIEF COMMUNICATION

Ecophysiological responses to neighbor removal in an old-field and a prairie in northeastern Kansas, USA

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Abstract

An ecophysiological approach was used to determine if competition can be detected among plants in a recently abandoned old-field and in a native tallgrass prairie in northeastern Kansas. *In situ* photosynthetic parameters and water potentials (Ψ) of target plants were measured 1-2 d after neighbor (intra- and interspecific) removal as well as 1-4 weeks later, and compared with values for plants with neighbors. Only two of the six study species (four old-field and two prairie species) responded to removal of neighboring plants, and only after several weeks had elapsed. Net photosynthetic rates (P_N) and stomatal conductances (g_s) of *Ambrosia trifida* in an old-field increased after removal of both intra- and interspecific neighbors. For *Apocynum cannabinum*, another old-field species, P_N of target plants without neighbors was significantly higher than that of target plants with neighbors. For both these species, values of Ψ were not different between target plants with and without neighbors, suggesting that increased availability of nutrients may have been responsible for the observed ecophysiological responses. Though numerous past studies indicate that competition is a major factor influencing plants in old-field and in prairie communities, the experimental approach used in this study revealed that neighbor removal had only limited effects on ecophysiology of the target plants in either community.

Additional key words: *Ambrosia trifida*; *Apocynum cannabinum*; *Aster pilosus*; competition; *Eryngium yuccifolium*; *Lespedeza capitata*; photosynthesis; *Solidago canadensis*; stomatal conductance; water potential.

Competition among plants has long been considered an important factor in the structuring of plant communities (Clements *et al.* 1929, Dwyer 1958, Fowler 1986, Goldberg and Barton 1992, Tilman 1994, Holmgren *et al.* 1997). Although ecologists

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**Author for correspondence; fax: 785-864-5321, e-mail: ecophys@falcon.cc.ukans.edu have extensively investigated plant-plant interactions using species removals, De Wit replacements, and nearest-neighbor analyses, few investigations of competition have incorporated ecophysiological approaches in the field. The few ecophysiological studies of competition located typically measured Ψ, g_s, or P_N following removal of neighboring plants (Sucoff and Hong 1974, Fonteyn and Mahall 1978, 1981, Robberecht *et al.* 1983, Ehleringer 1984, Bowman and Kirkpatrick 1986, Price *et al.* 1986, D'Antonio and Mahall 1991, Wang *et al.* 1995), yet only one such study included all three ecophysiological parameters (Price *et al.* 1986).

One ecophysiological approach that has received little attention for the investigation of competitive interactions between plants *in situ* involves comparing values of gas exchange and water relations of a target plant immediately after removal of its neighbors (intra- or interspecific) with the same set of values measured several weeks later. Measuring these parameters at two different times may allow differentiation of competition for water from competition for nutrients. For example, next-day measurements of ecophysiological parameters of the target plant should provide information regarding competition primarily for water. Measuring the same parameters again two weeks later should allow adequate time for changes in nutrient uptake and utilization to occur as a result of neighbor removal and should reflect possible competition for nutrients prior to neighbor removal, assuming, of course, that plants are well-hydrated at the time of measurement. In addition, the time between neighbor removal and the gas exchange measurements should be short enough to prevent degradation of allelopathic substances (Rice 1974) which could potentially confound interpretation of the results.

The goal of this research was to determine, using the *in situ* ecophysiological approach described above, if the ecophysiology of selected plants responded to removal of neighboring plants in an old-field and in a prairie. Immediate effects were compared with measurements made up to four weeks later in an effort to differentiate potentially increased availabilities of different resources.

Research was conducted on a 12.2 ha old-field during the late spring and throughout the summer of 1986 and 1987, and on a 4.6 ha native tallgrass prairie during mid- to late summer of 1987. Environmental values at these times are given in Norman (1989). At both research areas, all species selected were dominants or abundant in patches (old-field: *Ambrosia trifida* L., *Aster pilosus* Willd., *Apocynum cannabinum* L., and *Solidago canadensis* L.; prairie: *Eryngium yuccifolium* Michx. and *Lespedeza capitata* Michx.). Gas exchange and microenvironmental values were collected with a *LI-COR* (Lincoln, NE, USA) *LI-6000* Portable Photosynthesis System on sunny days using unshaded, healthy, mature leaves. Only physiological characteristics of target plants with leaf temperatures and relative humidities within 2 °C and 25 % of each other, respectively, were used in comparisons of P_N of plants with and without neighbors. Immediately following the measurement of P_N, Ψ was assessed on a nearby leaf using a Scholander-type pressure chamber (*PMS Instrument Co.*, Corvallis, OR, USA). Neighbors were removed at ground level within a 1 m (old-field) or 0.75 m (prairie) diameter circle centered on one target plant. Neighbors of the control plants were not disturbed. A smaller removal area was used in the prairie due to higher plant densities. Subsequent regrowth of neighbors was removed at least weekly in the old-field and more frequently in the prairie. Values were transformed (square-root, one-fourth root, *etc.*) when not normally-distributed or when heteroscedastic. One-way analysis of variance was used to test for differences among means, unless the transformed data were not normally distributed or heteroscedastic. In such cases, other parametric (two means with heterogeneous variances) or non-parametric (Mann-Whitney *U*-test) tests were utilized (Sokal and Rohlf 1981).

Table 1. *In situ* net CO_2 exchange rates (P_N) [μmol m^{-2} s^{-1}], leaf conductances to CO_2 (g_s) [mol m^{-2} s^{-1}], internal CO_2 concentrations (C_i) [μmol mol^{-1}], and leaf water potentials (Ψ) [MPa] of *Apocynum cannabinum* with and without interspecific neighbors (removed 15 or 20 d prior to measurements) at two different times during the growing season. Except where indicated (* indicates that two means are significantly different at $p < 0.05$), neighbor removal did not significantly affect physiological parameters (tested by one-way analysis of variance). Values are means ± SD of *n* individuals.

Date	Treatment	*n*	P_N	g_s	C_i	Ψ
6 June 1987	with neighbors	10	10.4 ± 2.3	0.5 ± 0.1	274 ± 11*	-1.33 ± 0.11
	20 d without neighbors	10	11.2 ± 2.1	0.4 ± 0.1	256 ± 20*	-1.31 ± 0.10
30 July 1987	with neighbors	20	9.9 ± 2.0*	0.5 ± 0.2	254 ± 14	-1.62 ± 0.23
	15 d without neighbors	18	11.6 ± 2.4*	0.5 ± 0.2	251 ± 13	-1.61 ± 0.21

For all species in both communities, the removal of neighbors had no effect on any of the physiological parameters measured from 0.5 to 72 h following neighbor removal (values not shown). On the other hand, the removal of neighbors in July 1987 resulted in increased P_N of *A. cannabinum* (accompanied by no changes in g_s and C_i) 15 d following neighbor removal (Table 1). In addition, after one of the two time intervals investigated, the presence of intra- and interspecific neighbors resulted in significantly lower P_N and g_s of *A. trifida* (Table 2). For both the above old-field species, as well as for the other four species, Ψ values of target plants, regardless of type of neighbor, were not significantly different from those of controls.

Removal of neighbors had no immediate or long-term (up to 28 d) effect on gas exchange parameters and water relations of the old-field species *A. pilosus* and *S. canadensis* (values not shown). Likewise, no effects of neighbor removal were observed with the two prairie species, *E. yuccifolium* and *L. capitata* (values not shown).

Thus, only two of the six species examined, *A. trifida* and *A. cannabinum*, both old-field species, responded to neighbor removal, although not in every instance. Given that this response was only observed after several weeks following neighbor removal, and that Ψ of the target plants with and without neighbors were not substantially different, it is unlikely that plants without neighbors were benefiting from a possible release from competition for water. Thus, the measured increase in photosynthesis following neighbor removal may reflect a release from competition for nutrients between these species and their neighbors.

Because only leaves in the upper canopy were chosen for P_N measurements, neighbor removal did not affect the interception of radiant energy by these leaves. Thus, competition for irradiation was considered unlikely as a mechanism underlying differences in physiological parameters found in this study.

Table 2. *In situ* net CO_2 exchange rates (P_N) [μmol m^{-2} s^{-1}], leaf conductances to CO_2 (g_s) [mol m^{-2} s^{-1}], internal CO_2 concentrations (C_i) [μmol mol^{-1}], and leaf water potentials (Ψ) [MPa] of *Ambrosia trifida* with and without intra- and interspecific neighbors (removed 10 or 28 d prior to measurements) in midsummer. Except where indicated (* indicates that two means are significantly different at $p < 0.05$; ** at $p < 0.01$; *** at $p < 0.001$), neighbor removal did not significantly affect physiological parameters (tested by one-way analysis of variance, unless otherwise indicated). Values are means ± SD of *n* individuals. [1]Test for two means with heterogeneous variances.

Date	Treatment	*n*	P_N	g_s	C_i	Ψ
(intraspecific)						
3 August 1986	with neighbors	8	18.1 ± 3.5*	0.7 ± 0.3*	253 ± 13[1]	-1.48 ± 0.12
	10 d without neighbors	7	23.0 ± 4.5*	1.0 ± 0.3*	253 ± 9[1]	-1.36 ± 0.13
25 August 1986	with neighbors	6	15.9 ± 4.4	1.0 ± 0.4	280 ± 14[1]	-1.37 ± 0.17
	28 d without neighbors	6	21.0 ± 5.2	1.2 ± 0.3	260 ± 9[1]	-1.40 ± 0.23
(interspecific)						
3 August 1986	with neighbors	8	19.2 ± 3.8	0.8 ± 0.4	249 ± 24	-1.44 ± 0.17
	10 d without neighbors	9	22.7 ± 3.3	1.0 ± 0.4	251 ± 16	-1.37 ± 0.13
25 August 1986	with neighbors	6	15.9 ± 4.1***	0.9 ± 0.4**	267 ± 30	-1.35 ± 0.19[1]
	28 d without neighbors	6	24.6 ± 2.2***	1.9 ± 0.5**	274 ± 29	-1.22 ± 0.03[1]

Past studies have reported evidence for competitive interactions among old-field species (Pinder 1975, Allen and Forman 1976, Armesto and Pickett 1986, Goldberg 1987, Miller and Werner 1987, Norman and Martin 1994, Wilson and Tilman 1995), as well as among prairie species (Hartnett 1993, Wedin and Tilman 1993, Van Auken *et al.* 1994, Gibson and Skeel 1996). In spite of these findings, evidence for competition in the current study was weak for old-field plants and non-existent for the prairie species. It is possible that competition was not detected in some cases as a result of the experimental approach used. For example, root systems of potential competitors were not removed and, even with their shoots removed, might have prevented release from competition. Also, the amount of time that elapsed between neighbor removal and the ecophysiological measurements could have been too short to allow competitive release. On the other hand, evidence for competitive interactions using this experimental approach was obtained with two species, and, in addition, potential insight into the nature of the competition between the plants was obtained. Thus, the ecophysiological approach holds promise as an additional tool in investigations of competitive interactions among plants.

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