Letter to the Editor

Arbuscular Mycorrhizal Colonization and Border Cell Production: A Possible Correlation

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Arbuscular mycorrhizae (AM) are ubiquitous soil fungi that form symbiotic associations with many plant species, including most significant crop plants (2,41). The AM associations can increase plant growth, in many cases by enhancing phosphorus uptake from soils with low to moderate phosphorus availability (31). A given plant species' AM propensity, which is the extent the root system of an individual plant is colonized by the AM symbiont, may vary under different conditions (e.g., natural soils versus disturbed agricultural soils). This variability can arise from differences in AM inoculum composition, soil nutrient availability, and plant community composition (25). Plant families may be generally, although not perfectly, categorized by the AM propensities of plant species within that family (13,39). Many families in the order Caryophyllales are considered minimally or nonmycorrhizal; of these, Brassicaceae and Chenopodiaceae have received the most attention (39). Baylis (3) hypothesized that a species' mycorrhizal propensity is related to root morphology. Species with thick, unbranched roots and few root hairs are more heavily dependent on mycorrhizal associations, either endomycorrhizal or ectomycorrhizal, than are species with finely branched roots and numerous root hairs. The primary exception to the Baylis hypothesis is the family Ericaceae, the species of which have very finely branched roots in addition to large numbers of hyphal connections with ericacious endomycorrhizal fungi (16). Despite this exception, Baylis' connection between root anatomy and mycorrhizal propensity is a widely accepted generalization (26).

Many plants release metabolically active border cells (BC) from the root cap into the rhizosphere (17,19). These cells undergo differentiation upon separation from the root, including distinct patterns of gene expression (5). BC (previously referred to as "sloughed root cap cells") are defined as cells that are released into suspension by a brief immersion into water (18). Different plant families vary considerably in their capacity to produce BC, ranging from zero BC per root (e.g., Brassicaceae and Chenopodiaceae) to thousands of BC per root (e.g., Leguminoseae and Cucurbitaceae) (20). BC production is consistent between species within a given family (20), typically varying between 10 and 20%.

Hawes and Pueppke (20) determined the BC production levels of a number of species from a variety of families. Brigham et al. (5) presented the average BC production for a variety of families. In these studies, BC production was measured in aseptic, newly germinated seedlings. We surveyed mycorrhizal literature to collect AM colonization data for over 40 plant species. The published AM colonization data for many of the species were associated with the average BC production data of its family; this was appropriate, given the comparatively low variability of BC production within families (4,20). Wherever possible, however, the AM colonization data were associated with BC production values determined for that particular species (20). This collection of data is presented in Table 1. The AM percent colonization in our collection of references refers to the percent of AM colonized root fragments as determined by the line intersect method, a widely used measure of AM association (6). The AM colonization references used were taken for their consistency of data collection technique and breadth of species tested, rather than for any other criteria. The growth conditions under which the AM colonization data were collected varied; this broad-based data set was specifically desirable to fully test the suggestion of an AM-BC correlation.

The data from the literature lead us to hypothesize a connection between a family's AM propensity and its capacity to produce BC. The production of BC appeared to be strongly correlated with mycorrhizal colonization. In general, families that were BC capable had a mycorrhizal propensity, whereas families that were not BC capable were minimally or nonmycorrhizal (e.g., Brassicaceae and Chenopodiaceae). The data used to formulate this hypothesis also seemed to suggest that the range of AM propensity may follow the range of BC capability. Thus, plants that produce larger numbers of BC appeared to have a greater mycorrhizal propensity, whereas plants that produce fewer BC appeared to have a lesser mycorrhizal propensity.

Species in the family Amaranthaceae were shown to produce BC on the order of hundreds of BC per root, comparable with the established mycorrhizal family Solanaceae (4). On the basis of increasing evidence, AM colonization of species in this family is more widespread than was previously believed (28,33,34). An early review of the mycorrhizal status of plants (13) included Amaranthaceae in a list of families that were considered to be "possibly nonmycorrhizal or rarely mycorrhizal". Gerdemann's review (13) incorrectly cited Koch (22) as the basis for this assertion, because Koch (22) did not mention the family Amaranthaceae. In light of the most recent data regarding the mycorrhizal status of the family Amaranthaceae, this example of BC capability in a mycorrhizal family, previously thought to be nonmycorrhizal, tends to support our hypothesis.

The family Pinaceae also is of particular interest among the families surveyed for BC production (4,20). Species in the family Pinaceae were determined to produce 3,000 to 5,500 BC per root (20). The species in this family are known to exhibit a characteristically obligate dependence on ectomycorrhizal fungi in nature (16). This example of BC capability in a family with a strong ectomycorrhizal propensity suggests that our hypothesis may possibly be broadened to include ectomycorrhizal, as well as AM interactions. However, the larger data set of BC production by ectomycorrhizal plant species needed to reliably expand our hypothesis is lacking.

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There are other interesting physiological points about a possible AM-BC connection. Many plant-produced compounds are known to have a profound impact on soil pathogens, even at very low concentrations (27,40). Upon dissociation from the root, BC generate a novel complement of gene products that are rapidly released into the external medium (5). The area of the rhizosphere distal to the root cap where the majority of BC are distributed is also the primary site of root penetration by AM and by a variety of important fungal root pathogens (1,16,17,18). BC have been shown to be specifically chemoattractive to pythiaceaous fungi (14). Thus, we speculate that BC-produced bioactive compounds may influence the behavior of the mycorrhizal population in the rhizosphere. Conventional root studies probably exclude the BC and, therefore, exclude from consideration gene products generated exclusively in the BC (20). The hypothesis put forward by Brigham et al. (5), that BC constitute a uniquely specialized tissue of the root system, may have important implications for the role of BC-produced compounds in the establishment of mycorrhizal symbioses, as well as in the course of development of root pathogens.

TABLE 1. Arbuscular mycorrhizal (AM) colonization and border cell (BC) production

Family	Species	AM%[a]	BC[b]	Ref.
Leguminosae	*Glycine max*	77	3260*	36
Leguminosae	*Glycine max*	63	3260*	29
Leguminosae	*Glycine max*	63	3260*	35
Leguminosae	*Glycine max*	47	3260*	43
Cucurbitaceae	*Cucumis sativus*	69	3070*	30
Leguminosae	*Phaseolus vulgaris*	70	3070*	24
Leguminosae	*Phaseolus vulgaris*	58	3070*	8
Leguminosae	*Phaseolus vulgaris*	20	3070*	23
Leguminosae	*Coronilla varia*	85	3000**	9
Leguminosae	*Robinia hispida*	44	3000**	9
Leguminosae	*Robinia pseudacacia*	66	3000**	9
Leguminosae	*Trifolium repens*	88	3000**	23
Leguminosae	*Vicia sativa*	98	3000**	23
Malvaceae	*Gossypium hirsutim*	69	3000*	37
Malvaceae	*Gossypium hirsutim*	55	3000*	32
Leguminosae	*Pisum sativum*	70	2680*	21
Gramineae	*Zea mays*	73	2350*	23
Gramineae	*Zea mays*	20	2350*	10
Gramineae	*Agrostis tennuis*	41	2150**	9
Gramineae	*Dactylis glomerata*	38	2150**	9
Gramineae	*Festuca arudinaceae*	62	2150**	9
Gramineae	*Festuca ovina*	41	2150**	9
Gramineae	*Holcus lanatas*	84	2150**	9
Gramineae	*Lolium perenne*	46	2150**	9
Gramineae	*Poa annum*	30	2150**	23
Gramineae	*Poa compressa*	13	2150**	9
Gramineae	*Avena sativa*	78	1645*	38
Gramineae	*Avena sativa*	48	1645*	23
Gramineae	*Avena sativa*	28	1645*	42
Gramineae	*Secale cereale*	41	1485*	38
Gramineae	*Secale cereale*	35	1485*	21
Gramineae	*Triticum aestivum*	76	1195*	38
Gramineae	*Triticum aestivum*	70	1195*	12
Gramineae	*Triticum aestivum*	68	1195*	11
Gramineae	*Triticum aestivum*	50	1195*	21
Gramineae	*Triticum aestivum*	40	1195*	23
Agavaceae	*Yucca baccata*	45	1050**	9
Amaranthaceae	*Achyranthes aspera*	34	140**	28
Amaranthaceae	*Achyranthes aspera*	15	140**	28
Amaranthaceae	*Aerva javanica*	8	140**	28
Amaranthaceae	*Alternanthera sessilis*	64	140**	28
Amaranthaceae	*Amaranthus caudatus*	66	140**	28
Amaranthaceae	*Amaranthus caudatus*	2	140**	28
Amaranthaceae	*Amaranthus crucutus*	5	140**	28
Amaranthaceae	*Amaranthus gracilis*	47	140**	28
Amaranthaceae	*Amaranthus persica*	12	140**	28
Amaranthaceae	*Amaranthus spinosus*	35	140**	28
Amaranthaceae	*Celosia argentia*	60	140**	28
Amaranthaceae	*Celosia argentia*	26	140**	28
Amaranthaceae	*Celosia cristata*	46	133*	28
Amaranthaceae	*Celosia cristata*	41	133*	28
Solanaceae	*Capsicum annum*	38	63*	15
Solanaceae	*Solanum nigrum*	57	55**	23
Solanaceae	*Solanum tuberosum*	28	55**	42
Solanaceae	*Solanum tuberosum*	25	55**	23
Solanaceae	*Lycopersicon esculentum*	48	16*	23
Solanaceae	*Lycopersicon esculentum*	42	16*	7
Brassicaceae	*Arabidopsis thaliana*	15	0**	23
Brassicaceae	*Brassica napus*	0	0**	11
Brassicaceae	*Capsella bursa-pastoris*	1	0**	23
Brassicaceae	*Raphanus vulgaris*	3	0**	23
Chenopodiaceae	*Beta vulgaris*	2	0**	23
Chenopodiaceae	*Chenopodium album*	9	0**	23
Chenopodiaceae	*Spinacia oleracea*	1	0**	23

[a] AM% is percent root colonization.

[b] BC: Border cell production is in number of cells released per root. Border cell production data are species specific (*, Hawes and Pueppke [20]) or the average for the family (**, Brigham et al. [4]).

This is, to our knowledge, the first discussion of a positive association of AM colonization with BC production. Our hypothesis, that mycorrhizal colonization is correlated with BC production, should be evaluated by further experimentation. These experiments could include i) a more complete determination of the mycorrhizal status of species in the family Amaranthaceae; ii) measurement of BC production by species in verifiably nonmycorrhizal families other than the families Brassicaceae and Chenopodiaceae; iii) measurement of BC production by species in Ericaceae, a family with a strong ericoid endomycorrhizal propensity; iv) measurement of BC production by other species in Pinaceae, a family with a strong ectomycorrhizal propensity; and v) measurement of the AM propensity of mutants of characteristically mycorrhizal species that have been rendered incapable or less capable of producing BC.

The overall physiological significance of BC has not been fully elucidated, nor has the role of BC-produced compounds. Hopefully, an evaluation of our hypothesis will lead to a greater understanding of the role that BC and BC-produced compounds may play in the establishment of mycorrhizal associations.

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