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Effect of High pH on Foliar Chlorosis and Growth of Five *Betula* Species[1]

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Abstract

The relative alkalinity tolerances of yellow birch, sweet birch, river birch, paper birch, and Japanese white birch were evaluated by comparing foliar chlorosis and growth of seedlings irrigated for 56 days with either a pH 6.0 nutrient solution (control) or K_2CO_3-amended solutions adjusted to pH 7.3 or 8.3. Both visual ratings and SPAD-502 chlorophyll meter measurements were effective methods of quantifying the severity of alkalinity-induced foliar chlorosis. Eight weeks of the pH 8.3 treatment was more effective than 4 weeks of the same treatment or 4 or 8 weeks of the pH 7.3 treatment for detecting differences in alkalinity tolerance among the species. Treatment for 8 weeks with either pH 7.3 or 8.3 solutions increased foliar chlorosis of sweet, river, paper, and Japanese white birch seedlings relative to the control treatment, whereas yellow birch seedlings exhibited mild chlorosis only in the pH 8.3 treatment. Based upon severity of chlorosis, yellow birch was most tolerant of soil alkalinity, sweet birch was least tolerant, and river, paper and Japanese white birch were intermediate in tolerance. Stem relative growth rates and shoot and root cumulative dry mass values did not consistently corroborate the relative alkalinity tolerances of the birch species indicated by the chlorosis and chlorophyll data, possibly because of container restriction of root growth of the more rapidly growing species. Results of this study indicate that yellow birch may be valuable for developing new birch cultivars adapted to alkaline soils.

Index words: alkalinity, bicarbonate, landscape plants, foliar chlorosis.

Species used in this study: yellow birch (*Betula alleghaniensis* Britt.); sweet birch (*Betula lenta* L.); river birch (*Betula nigra* L.); paper birch (*Betula papyrifera* Marsh.); Japanese white birch *(Betula platyphylla* var. *japonica* Hara.).

Significance to the Nursery Industry

Many popular birch species and cultivars grow poorly and develop extensive foliar chlorosis when planted in alkaline soils. Results of this study demonstrate that genetic variation for alkalinity tolerance exists within the genus *Betula* and can be detected using a simple and inexpensive methodology. Use of this system to screen seedling populations of birch species with valuable landscape characteristics could facilitate breeding and selection of new cultivars with improved tolerance to high pH soils.

Introduction

Valued for their attractive bark, colorful fall foliage, and availability as single-stemmed or multi-trunked specimens, birch taxa are commonly planted as landscapes trees in much of the northern and eastern United States (9). However, some birch species are intolerant of high soil pH and are therefore unsuitable for areas where alkaline soils predominate. Even in regions where native soils are acidic, use of birch may be impractical where localized pockets of alkaline soil occur as a result of construction practices that expose calcareous subsoils, or where precipitation and irrigation runoff from limestone and concrete surfaces raise soil pH (29, 31).

While the growth and development of many tree taxa are adversely affected by high soil pH, genetic variation for alkalinity tolerance has been reported for some genera (9, 27, 31), thus presenting opportunities for selection of adapted genotypes. To date, most efforts to screen for tolerance to alkaline conditions have focused on rootstocks for commercial fruit production (3, 6, 10, 15, 27), while the range of adaptability present in most landscape tree species remains unexplored. Effective screening of large seedling populations for alkalinity tolerance requires that treatment and evaluation protocols be simple, inexpensive, and reproducible. Bicarbonate plays an important role in inducing foliar chlorosis in many plant species growing in alkaline soils (2, 8, 20). Shi and Byrne (27) reported that irrigation of *Prunus* seedlings with potassium carbonate-amended nutrient solution followed by visual evaluation or chlorophyll meter measurements of chlorosis provided an efficient method of separating tolerant from susceptible genotypes. If equally effective with birch species, this technique could be used to characterize the relative alkalinity tolerance of taxa with valuable ornamental attributes and facilitate breeding and selection of cultivars adapted to high pH soils.

The objectives of this study were 1) to evaluate the efficacy of irrigation with bicarbonate-amended nutrient solutions as a means of inducing alkalinity stress in birch seedlings, 2) to determine the validity of using a SPAD-502 chlorophyll meter and/or a visual rating system for quantifying foliar chlorosis in birch seedlings, and 3) to characterize the relative alkalinity tolerance of yellow birch, sweet birch, paper birch, Japanese white birch, and river birch seedlings. River birch is generally considered to be intolerant of high soil pH (9, 12, 16) and was included in this study as a standard for comparison. Both sweet birch and paper birch reportedly prefer slightly acidic soil (9), although paper birch purportedly tolerates high pH (9) and highly calcareous (16) soils. Yellow birch is commonly found growing on calcareous soils and has been described as tolerating a wide range of soil pH (16). Little is known about the pH tolerance of Japanese white birch.

Materials and Methods

Seeds were collected in the spring and fall of 1996 from open-pollinated trees of yellow birch, sweet birch, paper birch, Japanese white birch, and river birch growing at the

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University of Minnesota Landscape Arboretum in Chanhassen, MN. When possible, seeds were collected from isolated plantings of a species to reduce the likelihood of including interspecific hybrid seedlings in the study. The origins of the female parents of the seedlings used in this study were as follows: yellow birch—a native seedling from Interstate State Park, St. Croix Falls, WI; sweet birch—a seedling grown from seed received from Ag Canada, Central Experiment Station, Ottawa, provenance unknown; river birch—seed source unknown; paper birch—a native seedling from Ely, MN; Japanese white birch—two 'Whitespire' trees purchased from a commercial nursery. Seeds were moist-chilled (cold stratified) for 30 days at 4C (39F) and sown in a greenhouse in mid-January, 1997. Supplemental light was provided daily for 16 hours with high pressure sodium lamps. Daily maximum and minimum air temperatures were 27 ± 4 and 22 ± 3C (81 ± 6 and 72 ± 5F), respectively.

Two-week-old seedlings were transplanted into individual 40-ml cells containing a peat-based growing medium (Pro-Mix; Premier Brands Inc; Red Hill, PA). Within each species, seedlings with atypical leaf shapes or quantities of leaf or stem pubescence were discarded. Plants received a weekly application of liquid fertilizer (Peters Excel 21N–2.2P–16.4K (21–5–20), Grace-Sierra Co., Milipitas, CA) containing 200 mg/liter N at a pH of 6.0. Five-week-old seedlings were transplanted into 3.2 liter (No.1) hexagonal containers containing a vermiculite:perlite (2:1 by vol) mixture. Sides of the container drainage holes were taped to prevent loss of the growing medium without impeding drainage. Plants were fertilized weekly as described above.

When the seedlings were ten weeks old, 39 uniform plants of each species were randomly assigned to the pH 6.0 (control), pH 7.3, or pH 8.3 treatments. The pH treatment solutions were prepared using distilled water containing a complete fertilizer (Peters Excel 21N–2.2P–16.4K (21–5–20)) at 100 mg/liter N and the following amendments: 1) pH 6.0: no additional amendments; 2) pH 7.3: 0.125 g K_2CO_3/liter; 3) pH 8.3: 0.25 g K_2CO_3/liter. The final pH of each solution was adjusted with 10 M KOH.

High soil moisture levels can increase soil bicarbonate content and exacerbate alkalinity-induced foliar chlorosis of woody taxa (2). Shi and Byrne maintained a moist growing medium to distinguish between *Prunus* genotypes tolerant and susceptible to bicarbonate-induced iron chlorosis (27). In a preliminary experiment, maintaining the growing medium in a near-saturated condition expedited development of foliar chlorosis in birch seedlings irrigated with K_2CO_3-amended solution without deleteriously affecting normal growth and development of control treatment plants. In the current study, individual plastic trays were placed beneath each container to maintain a shallow (approximately 2 cm (0.79 in) deep) reservoir of nutrient solution in contact with the growing medium. Seedlings were placed on two adjacent greenhouse benches at a spacing of 46 cm (18.1 in) on-center. Each container was flushed with 3 pot volumes of the appropriate nutrient solution and watered thereafter every 2–3 days with the same solution. This irrigation frequency effectively maintained the growing medium pH within ± 0.3 pH units of the treatment solution pH. To prevent a buildup of soluble salts in the growing medium, the trays were removed and the containers flushed with 3 pot volumes of deionized water approximately every 2 weeks. After draining for 2 hours, the containers were flushed again with 3 pot volumes of the appropriate treatment solution before being placed back inside the trays.

Temperature and photoperiod conditions were maintained as described previously. Levels of photosynthetically active radiation 46 cm above the bench surface ranged from 250 to 1250 µmole m^{-2} s^{-1}.

Emerging lateral branches were removed from the seedlings as needed throughout the experiment to maintain a dominant central leader. The height of each seedling was measured just prior to the initial irrigation with the pH treatment solutions and again after 42 days of treatment for calculation of stem relative growth rates.

Leaf chlorosis of the three most recently expanded leaves was measured on day 28 and day 55 of the experiment using a chlorophyll meter (SPAD-502; Minolta Corp.). Six readings were taken per leaf and the average of all 18 readings was recorded. Chlorosis of these leaves was also rated visually on day 55 using a scale similar to that used by Shi and Byrne (27) with 1 = green leaves with no chlorosis; 2 = green leaves with slightly yellow interveinal areas; 3 = most of the interveinal region is yellow, but veins are green; 4 = entire interveinal region is distinctly yellow, veins are pale green to yellow; and 5 = entire leaf is yellow to white. Leaf chlorophyll content was measured 56 days after initiation of treatment. Six 11-mm- (0.43 in) dia disks were collected with a cork borer from each of the 2 most recently fully expanded leaves of 10 plants in each species × pH treatment combination. Leaf disks were placed in light-excluding vials containing 10 ml of DMSO (dimethyl sulfoxide) and heated for 18 hours at 70C (158F) (17). A spectrophotometer (Beckman DU 50) was used to measure optical densities of the extracts at 645 and 663 nm and chlorophyll content was calculated using the equation of Arnon (1).

On day 56, the 3 most recently expanded leaves were collected from 3 seedlings of yellow, sweet, and river birch in each pH treatment for foliar nutrient analysis. Leaves were rinsed with distilled water, oven dried for 72 hours at 70C (158F), ground, digested with 10% HCL (dry ash method) and analyzed at the University of Minnesota Research Analytical Laboratory using inductively coupled plasma-atomic emission spectroscopy.

Plants were harvested on day 57 and total leaf area of each plant was measured with a leaf area meter (LI-COR, Inc. Lincoln, NE). Roots were gently washed free of growing medium and the dry mass of roots, leaves and stems were determined after oven drying for 72 hours at 70C (158F). Areas and dry masses of leaves used for chlorophyll and nutrient content determinations were included in the totals.

Experimental design: A completely randomized design was used with treatments applied in a 5 × 3 factorial with 5 species and 3 pH levels and 13 plants per treatment combination. Data were subjected to analysis of variance procedures and mean separation was calculated using Fisher's LSD, $P \leq 0.05$.

Results and Discussion

Based upon measurements of leaf chlorosis (Table 1) and seedling growth (Tables 2 and 3), irrigation with K_2CO_3-amended nutrient solution was effective at inducing alkalinity stress in the birch seedlings. Alkalinity-induced foliar chlorosis of tree species is typically caused by deficiencies of iron and/or manganese (21, 24). Foliar nutrient analysis results indicated that uptake and/or translocation of these two

nutrients was reduced in plants in the two higher pH treatments (Table 2). In general, leaf chlorophyll content and growth were more reduced by the pH 8.3 treatment than the 7.3 treatment. Differences in severity of chlorosis among the species were detected in the higher pH treatment, indicating that effective screening of seedling populations could be accomplished using the pH 8.3 solution exclusively. Further work is required to determine the optimal treatment duration. Shi and Byrne (27) were able to distinguish between resistant and susceptible *Prunus* genotypes after approximately 4 weeks of treatment, whereas differences among the birch species in this study were much more easily discerned after 8 weeks of treatment than 4. Chlorosis evaluations were not performed in between these two times, however, and considerable time savings might be realized if the efficacy of a shorter treatment period was established.

SPAD-502 readings were positively correlated with leaf chlorophyll content measurements expressed on either a leaf fresh mass or leaf area basis (r = 0.89 and 0.88, respectively). Because chlorophyll distribution can be highly variable within a leaf (23), the correlation between SPAD-502 readings and actual chlorophyll content would likely have been stronger had meter readings been confined to the leaf disks harvested for chlorophyll analysis. However, the results are in agreement with earlier findings on red maple (*Acer rubrum* L.) (28) and numerous herbaceous species (18, 23, 28, 32) and validate the use of this simple, nondestructive technique for estimating leaf chlorophyll levels in birch seedlings. SPAD-502 readings also correlated highly with visual ratings of chlorosis (r = 0.96), supporting Shi and Byrne's (27) finding that visual chlorosis ratings are suitable for evaluating seedling responses to high pH. SPAD-502 measurements would be preferable for maintaining consistency when multiple persons are involved in rating seedlings or when comparative evaluations are temporally separated.

Based upon SPAD-502 readings, sweet, river, and paper birch seedlings treated for 4 weeks with either the pH 7.3 or 8.3 solutions and Japanese white birch seedlings treated for 4 weeks with the pH 8.3 solution were more chlorotic than control treatment seedlings (Table 1). However, yellow birch seedlings exhibited little chlorosis after 4 weeks in either the pH 7.3 or 8.3 treatment. Seedlings of all species irrigated for 8 weeks with the pH 7.3 or 8.3 solutions were more chlorotic than corresponding control seedlings, but the severity of chlorosis differed among species (Table 1). SPAD-502 values of yellow birch seedlings in the pH 7.3 and 8.3 treatments were 9 and 20% lower, respectively, than that of control plants (visual chlorosis ratings and leaf chlorophyll concentrations of yellow birch seedlings in the control and pH 7.3 treatments did not differ significantly), whereas similarly treated sweet birch seedlings had SPAD-502 values 74 and 80% lower than control plants. River, paper and Japanese white birch seedlings also were more chlorotic than yellow birch seedlings after 8 weeks in the pH 7.3 and 8.3 treatments. Based upon severity of foliar chlorosis, yellow birch was most tolerant of soil alkalinity, sweet birch was least tolerant, and river, paper and Japanese white birch were intermediate in tolerance.

Because leaf photosynthetic surface is the source of carbohydrates essential for plant growth, foliar chlorosis will inevitably have an adverse effect on growth over time. Byrne (5) reported that a *Prunus* rootstock resistant to alkaline conditions experienced no growth reduction at a soil pH of 8.0, whereas a susceptible genotype exhibited a 62% decrease in

Table 1. SPAD-502 measurements, visual chlorosis ratings, and leaf chlorophyll content of five *Betula* species treated with pH 6.0 nutrient solution (control) or K_2CO_3-amended nutrient solutions adjusted to pH 7.3 or 8.3.

Species	pH	SPAD-502[z] (Week 4)	SPAD-502[z] (Week 8)	Visual rating	Chlorophyll content ng cm^{-2}	Chlorophyll content mg gfw^{-1}
Betula alleghaniensis	6.0	27.4a[y]	28.8a	1.0a	18.7a	1.30a
	7.3	27.5a	26.3b	1.2a	18.8a	1.29a
	8.3	26.9a	23.0c	1.8b	18.2a	1.08b
Betula lenta	6.0	29.1a	29.7a	1.0a	17.3a	1.41a
	7.3	24.1b	7.8b	3.7b	3.5b	0.27b
	8.3	17.4c	6.0b	3.9b	3.9b	0.26b
Betula nigra	6.0	30.3a	30.8a	1.0a	22.3a	1.49a
	7.3	24.6b	17.3b	2.5b	15.1b	0.95b
	8.3	16.6c	9.7c	3.5c	13.9b	0.81b
Betula papyrifera	6.0	27.6a	29.1a	1.2a	19.4a	1.05a
	7.3	23.0b	14.4b	2.7b	10.4b	0.59b
	8.3	21.1b	9.0c	3.7c	8.1b	0.41c
Betula platyphylla var. *japonica*	6.0	25.9a	28.2a	1.1a	19.1a	1.20a
	7.3	22.1a	12.8b	3.1b	9.0b	0.61b
	8.3	17.8b	8.8b	3.5b	8.6b	0.52b
Analysis of variance						
Species		**	**	**	**	**
pH		**	**	**	**	**
Species × pH		**	**	**	**	**

[z]All variables were measured after 8 weeks of treatment; SPAD-502 measurements were also made after 4 weeks of treatment. Visual ratings were assigned using the following scale: 1 = green leaves with no chlorosis; 2 = green leaves with slightly yellow interveinal areas; 3 = most of the interveinal region is yellow, but veins are green; 4 = entire interveinal region is distinctly yellow, veins are pale green to yellow; and 5 = entire leaf is yellow to white.

[y]Mean separation by species within columns by Fisher's LSD (P = 0.05); n = 13.

Table 2. Stem relative growth rates (mm cm^{-1} day^{-1}) of seedlings of five birch species irrigated for 42 days with either pH 6.0 nutrient solution (control) or K_2CO_3-amended nutrient solution adjusted to pH 7.3 or 8.3.

Species	Irrigation solution pH		
	6.0	7.3	8.3
B. alleghaniensis	0.28a[z]	0.28a	0.26a
B. lenta	0.23a	0.23a	0.18b
B. nigra	0.28a	0.26ab	0.23b
B. papyrifera	0.24a	0.25a	0.24a
B. platyphylla jap.	0.26a	0.25ab	0.23b

[z]Mean separation within species by Fisher's LSD (P = 0.05); n = 13.

shoot dry mass and a 22% reduction in plant height relative to the control. Blueberry (*Vaccinium* species) seedlings grown at pH 6.0 accumulated less dry mass than those grown at pH 5.0, while plant height was unaffected by pH (11). Stem relative growth rates (RGRs) of the five birch species were affected differently by pH treatment over the 42-day measurement period (Table 2). RGRs of yellow and paper birch were similar in all pH treatments, whereas sweet, river, and Japanese white birch seedlings had significantly lower RGRs in the pH 8.3 treatment than in the control treatment.

At harvest, cumulative shoot dry masses of all species were significantly lower in the pH 7.3 and 8.3 treatments than in the control treatment (Table 3). Although differences among species were not statistically significant, shoot dry masses of yellow, paper, and Japanese white birch seedlings in the pH 8.3 treatment tended to be reduced less relative to the control treatment (–25%, –8%, and –25%, respectively) than those of sweet and river birch seedlings (–52%, –43%, respectively). The effect of pH on root dry mass differed among species (significant species × pH interaction, P = 0.05). Root dry masses of yellow birch, paper birch and Japanese white birch seedlings were not affected by pH treatment; dry masses [mean (± sem)] of these 3 species in the control and pH 8.3 treatments were 5.9 (0.5) and 6.5 (0.4) g, 10.0 (0.8) and 11.2 (0.5) g, and 7.8 (0.7) and 8.4 (0.5) g, respectively. Sweet and river birch seedlings had greater root dry mass in the control treatment (5.1 (0.3) and 5.1 (0.4) g, respectively) than in the pH 8.3 treatment (3.9 (0.3) and 4.1 (0.4) g, respectively).

Root to shoot and root to leaf area ratios increased for all five species with increasing treatment pH (Table 3). However, the biological significance of this phenomenon is unclear. Woody plants experiencing water stress frequently exhibit a similar shift in carbohydrate allocation that favors root development relative to shoot growth and facilitates maintenance of a favorable internal moisture balance (13, 14, 22). A high root to shoot ratio conceivably could benefit plants in alkaline soils as well, by combining greater root surface area for nutrient absorption with lessened total nutrient demand. However, we detected no obvious relationship between root to shoot or leaf area to root dry mass ratios and the relative sensitivities of the birch species to high pH. Sweet birch seedlings in the pH 8.3 treatment had the highest mean root to shoot ratio but were also the most chlorotic, indicating that the shift in carbohydrate allocation was of little direct adaptive value.

Growth measurements did not consistently corroborate the relative alkalinity tolerances of the birch species indicated by the chlorosis and chlorophyll data. Yellow birch seedlings generally grew better in the pH 7.3 and 8.3 treatments than the more chlorotic sweet and river birch seedlings. However, the relatively minor impact of the 2 alkaline treatments on growth of paper birch and Japanese white birch seedlings was inconsistent with the degree of chlorosis exhibited by these 2 species. This discrepancy may have been a consequence of container restriction of root growth as the seedlings increased in size (25, 30). Seedlings of paper and Japanese white birch were larger than those of the other species at initiation of treatment (data not shown). Consequently, the true effect of the alkaline treatments on paper birch and Japanese white birch may have been masked by a reduction in growth of control treatment seedlings of these species as soil volume became restrictive. The pH-adaptability of Japanese white birch has not, to our knowledge, been characterized previously. The degree of chlorosis exhibited by this species in both the pH 7.3 and 8.3 treatments indicates that it is relatively intolerant of alkaline conditions. Paper birch purportedly possesses a degree of alkalinity tolerance (9, 16). While

Table 3. Cumulative growth and foliar iron and manganese concentrations (mg kg^{-1}) in terminal leaves of *Betula* species harvested after 56 days of treatment with pH 6.0 nutrient solution (control) or K_2CO_3-amended nutrient solution adjusted to pH 7.3 or 8.3.

	Dry mass (g)						Foliar nutrient concentration (mg kg^{-1})	
	Root	Shoot	Whole plant	Leaf area (cm^2)	Stem length (mm)	Root:shoot ratio	Fe	Mn
Species								
B. alleghaniensis	6.0	15.1c[z]	21.1c	1761b	925b	0.41b	145a	222b
B. lenta	4.8	10.6d	15.4d	1235c	770c	0.50a	86b	364a
B. nigra	4.6	11.3d	15.9d	942c	964b	0.43b	58b	290ab
B. papyrifera.	10.4	33.2a	43.6a	3202a	1122a	0.32c	—	—
B. plat. japonica.	8.3	23.4b	31.7b	2068b	1156a	0.37bc	—	—
pH								
6.0	6.8	21.3a	28.1a	2023a	1028a	0.34c	125a	489a
7.3	6.9	18.9b	25.8a	1933a	1013a	0.40b	92ab	220b
8.3	6.8	15.9c	22.7b	1567b	921b	0.48a	73b	167b
Analysis of variance								
Species	**	**	**	**	**	**	**	**
pH	NS	**	**	**	**	**	**	**
Species x pH	*	NS	NS	NS	NS	NS	NS	NS

[z]Mean separation by species or pH within columns by Fisher's LSD (P = 0.05); n = 13. For nutrient values, n = 3.

the growth data support this supposition, the extensive chlorosis induced by the two alkaline treatments suggests that paper birch is comparable to Japanese white birch in its sensitivity to high soil pH. It is important to note that ecotypic and genotypic variation in pH adaptability may exist within the species we tested and could account for discrepancies in characterizations of their pH adaptability.

The results of this study support anecdotal characterizations of yellow birch as possessing a degree of tolerance to alkaline soil conditions. Although not completely immune to the effects of high pH and bicarbonate, its performance was superior to that of the other species evaluated. Yellow birch may merit greater use as a landscape tree in regions of the country with cool summer climates and adequate soil moisture. However, due to its relative intolerance of high temperatures (9, 16) and waterlogged soils (16, authors' observations from greenhouse flooding trials), yellow birch may ultimately prove to be most valuable for hybridization with other species. Purportedly more resistant to bronze birch borer [*Agrilus anxius* (Gory)] (26) and birch leaf miner [*Fenusa pusilla* (Lepeletier)] (19) than most white-barked species, it has been successfully crossed with several white-barked birch species in efforts to create white-barked selections with good insect resistance (Tom Ranney, North Carolina State University; Brent McCown, University of Wisconsin, personal communications). Our findings suggest that progeny of these crosses may also be better adapted to alkaline soils than their white-barked parents. Potential also may exist for crossing yellow birch with river birch (7) to develop cultivars adapted to both alkaline and waterlogged soil conditions.

Sweet birch appeared to be the least alkalinity tolerant of the species evaluated, while paper and Japanese white birch performed comparably to river birch, our alkalinity intolerant standard. Several physiological mechanisms have been identified that enhance a plant's ability to tolerate high soil pH (4). Investigating the underlying basis for the differing tolerances of the birch species was beyond the scope of this study, but the range of responses detected may represent an opportunity for future study of woody plant adaptations to soil alkalinity. Because the comparisons made in this study were based upon a single population of each species, further work also is warranted to evaluate the range of genetic variation extant in these and other birch species with potential for use as landscape trees. Screening of populations derived from ecotypes growing in diverse habitats, especially calcareous sites, should facilitate selection of genotypes with maximum alkalinity tolerance.

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