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TRANSPLANTING NATIVE DOMINANT PLANTS TO FACILITATE COMMUNITY DEVELOPMENT IN RESTORED COASTAL PLAIN WETLANDS

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Abstract: Drained depressional wetlands are typically restored by plugging ditches or breaking drainage tiles to allow recovery of natural ponding regimes, while relying on passive recolonization from seed banks and dispersal to establish emergent vegetation. However, in restored depressions of the southeastern United States Coastal Plain, certain characteristic rhizomatous graminoid species may not recolonize because they are dispersal-limited and uncommon or absent in the seed banks of disturbed sites. We tested whether selectively planting such wetland dominants could facilitate restoration by accelerating vegetative cover development and suppressing non-wetland species. In an operational-scale project in a South Carolina forested landscape, drained depressional wetlands were restored in early 2001 by completely removing woody vegetation and plugging surface ditches. After forest removal, tillers of two rhizomatous wetland grasses (*Panicum hemitomon*, *Leersia hexandra*) were transplanted into single-species blocks in 12 restored depressions that otherwise were revegetating passively. Presence and cover of all plant species appearing in planted plots and unplanted control plots were recorded annually. We analyzed vegetation composition after two and four years, during a severe drought (2002) and after hydrologic recovery (2004). Most grass plantings established successfully, attaining 15%–85% cover in two years. Planted plots had fewer total species and fewer wetland species compared to control plots, but differences were small. Planted plots achieved greater total vegetative cover during the drought and greater combined cover of wetland species in both years. By 2004, planted grasses appeared to reduce cover of non-wetland species in some cases, but wetter hydrologic conditions contributed more strongly to suppression of non-wetland species. Because these two grasses typically form a dominant cover matrix in herbaceous depressions, our results indicated that planting selected species could supplement passive restoration by promoting a vegetative structure closer to that of natural wetlands.

Key Words: depressional wetlands, *Leersia hexandra*, *Panicum hemitomon*, revegetation, wetland restoration

INTRODUCTION

Restorations of depressional wetlands generally have used "passive" approaches for establishing desired vegetation (Galatowitsch and van der Valk 1996, Barton et al. 2004). In depressions altered by tiling or ditching, hydrology is restored by breaking tiles and plugging ditches. Natural colonization from remnant seed banks and seed dispersal is then relied upon to establish wetland plant species, under the assumption that restored hydrologic conditions can selectively favor these species and exclude undesired non-wetland species (Mitsch and Wilson 1996). Successful passive revegetation would reduce the need for more expensive seeding or multi-species plantings. However, even if existing seed banks prove adequate to restore a functional wetland plant community, there are at least two potential limitations (Galatowitsch and van der Valk 1996, De Steven et al. 2006). First, restored vegetation may differ from that of natural (reference) wetlands because the remnant seed banks may lack characteristic species or species guilds, particularly those that disperse poorly and propagate vegetatively. Second, site preparations favoring seed bank emergence can simultaneously allow undesired species to colonize. Annual cover crops have been tested as a means to suppress unwanted species in sedge meadow restorations, but with limited success (Perry and Galatowitsch 2003). Another approach is selective reintroduction of native perennial wetland species that would not otherwise recolonize restored sites (Fraser and Kindscher 2001, Budelsky and Galatowitsch 2004; see also Simmons 2005).

We explored this concept within the framework of a large project testing passive restoration methods in small Coastal Plain depressions on the U. S. Department of Energy's Savannah River Site (SRS) in South Carolina, USA. The experimental project has been described fully elsewhere (Barton et al. 2004, De Steven et al. 2006). It used 16 small, isolated depressional wetlands that had been ditched and drained historically but then abandoned from agricultural use; after abandonment, the sites had developed successional forest with facultative (FAC; Reed 1988) tree species indicative of drained sites (Kirkman et al. 1996). Herbaceous understory vegetation in these sites was sparse to absent (De Steven et al. 2006). Restoration initiated in 2001 consisted of clear-cutting the successional forest to open the sites and expose soils for revegetation, and plugging the ditches to raise water levels and lengthen ponding durations. The expectation was that wetland emergent species would establish naturally from existing seed banks and seed dispersal.

Results indicated that initial colonizers of the restored sites were native wet-meadow perennials and mudflat annuals that were common in the seed banks and that produce abundant seed; native upland ruderals with wind-dispersed seeds also colonized early (De Steven et al. 2006). A majority of the vegetative cover was wetland (OBL, FACW) species, consistent with the restoration goals. However, some characteristic species of natural herbaceous depressional wetlands failed to colonize the restored sites, notably maidencane grass (*Panicum hemitomon* Schult.), southern cutgrass (*Leersia hexandra* Sw.), and peatland sedge (*Carex striata* Michx). These native obligate wetland (OBL) species are perennial rhizomatous graminoids that often form a vegetative matrix of 50%–90% cover within undisturbed herbaceous depressions (De Steven and Toner 2004); however, they are generally poorly represented or absent in the seed banks and vegetation of drained depressions (Singer 2001, De Steven et al. 2006; see also Wetzel et al. 2001). Lacking wind-borne seeds, these species are unlikely to recolonize restored isolated depressions without active reintroduction. Therefore, when the restoration project was established in early 2001, we also conducted a small experiment to test whether we could successfully plant two of these wetland dominants (*L. hexandra*, *P. hemitomon*) to promote a vegetative matrix more closely resembling that of natural herbaceous depressions. We used rooted tiller transplants (Steed and DeWald 2003) because attempts to establish these grasses and some wetland sedges from seed or rhizomes have given mixed or poor results (P. Stankus, unpublished data; S. P. Miller, personal communication; van der Valk et al. 1999, Yetka and Galatowitsch 1999). In designing the experiment, we hypothesized that successful grass plantings could facilitate restoration of wetland vegetation in two ways: 1) by achieving more rapid cover development compared to natural colonization alone, and 2) by reducing the presence and cover of non-wetland plant species.

METHODS

Study Area

The 80,000-ha SRS is a U.S. Department of Energy National Environmental Research Park located on the South Carolina Upper Coastal Plain. Most of the SRS is comprised of managed and unmanaged forests, within which occur approximately 300 Carolina bays and similar depressional wetlands of various sizes (Kilgo and Blake 2005). The regional climate is humid subtropical; mean annual rainfall is 1200 mm, but multi-year droughts occur periodically. A seven-month growing season extends approximately from the end of March to the end of October. Depressional wetland hydrology is seasonal: water levels increase during winter to early spring highs, then decline at varying rates as growing-season evapotranspiration increases. Annual hydroperiods (ponding durations) are rainfall-dependent and become shorter during droughts (Mulhouse et al. 2005). During this study, below-normal rainfall and drought conditions occurred in 2001–2002; drought ended with the return of increased rainfall in 2003–2004 (De Steven et al. 2006).

Planting Experiment and Analysis

We used 12 of the 16 project wetlands for the transplanting experiment. Project wetlands were distributed across the SRS within forested uplands. All wetlands were relatively small (0.5–2 ha) and still drained via outflow ditches when restoration was started (details in Barton et al. 2004, De Steven et al. 2006). All had similar soils (Arenic or Typic Ochraquults) with sandy surface horizons and finer-textured subsoils (C. D. Barton, unpublished data). Removal of forest cover from the wetlands was completed by February 2001; ditch plugging was completed later in the year, but there were little to no water outflows in the interim because of the drought. Starting in the pre-restoration year (2000), water levels at the deepest center point in each wetland were monitored with continuous recording wells and staff gauges, and annual hydroperiods (percent of days ponded at depth > 0) were calculated for each wetland (data from C. D. Barton).

Between late April and early May 2001, *Leersia hexandra* and *Panicum hemitomon* were collected on the SRS from saturated or shallow-water fringe areas in herbaceous wetlands where the species were locally abundant. (We did not experiment with *Carex striata* because source material was scarce on the SRS). Both grass species have a spreading growth habit and may form extensive stands, but *Panicum* is taller and has stouter culms (Mulhouse et al. 2005). At the time of collection, the two grasses had emerged from overwintering rhizomes; shoot heights were typically about 25 cm and 35 cm for *Leersia* and *Panicum*, respectively. Grass sods were excavated with hand trowels or shovels, broken apart into small tiller-transplants (2–3 shoots plus attached roots), and placed individually into narrow open-topped polyethylene bags (12.5 cm wide $\times$ 22 cm tall) that kept the roots moist. We obtained each species from three donor wetlands and mixed the bags so that each experimental wetland received transplants from multiple donor sites. Bagged transplants were stored temporarily in covered bins in a dark cold chamber for 1–2 days until outplanting, which was completed between April 27 and May 9, 2001.

We established one planting block in each of the 12 restored wetlands. All wetlands had ponded shallowly (mean depth = 31 cm) after some March rains, but by late April they were drying down and exposing the bare soils. Because restored ponding depths could not be predicted, we placed each block near the water's edge at the time of outplanting (i.e., either centrally or peripherally within the basin depending on whether the wetland was already nearly dry or was still ponded) to equalize future ponding levels among blocks. This proved reasonably effective, as water depths measured in the blocks during a high-water year (2003) did not differ by block placement ($t = 0.5$, $df = 10$, n.s.). Block size was proportionate to wetland size, with dimensions ranging from 18 m $\times$ 9 m to 20 m $\times$ 15 m and with the longer dimension parallel to the water line and wetland perimeter. We cleared the blocks of large coarse woody debris remaining after harvest. Each block was divided lengthwise into two half-blocks, with each grass species randomly assigned to a half-block. We used dibble bars to hand-plant the tillers at spacings of 0.61 m (2 ft) and 0.76 m (2.5 ft) for the smaller *Leersia* and the larger *Panicum*, respectively (densities of approximately 3 m^{-2} and 2 m^{-2}). Previous trials suggested that these densities would allow for successful lateral spread while limiting the number of transplants needed (Wein et al. 1987). Across all wetlands, totals of 3,020 *Leersia* and 2,200 *Panicum* tillers were planted. We estimated attained grass coverage (see following) as a measure of planting success, because the spreading growth habit quickly obscured the identity of individual transplants. We later discovered that the *Panicum* planting stock had also contained tillers of the wetland grass *Sacciolepis striata* (L.) Nash (formerly *Panicum striatum* or *P. gibbum*; Hitchcock and Chase 1950), an ecologically similar species that is nearly indistinguishable from *P. hemitomon* in the vegetative condition. For simplicity we refer to this mixed stock as ''*Panicum*''.

For vegetation sampling, we established a 4-m^2 (2 m $\times$ 2 m) plot in the center of each planted half-block (one each for *Leersia* and *Panicum*) and paired these with a comparable 4-m^2 control plot (unplanted, natural colonization only) randomly placed adjacent to the planted block. In August of each year through 2004, we estimated cover class of each species present in the plots (including the planted grasses) using the 7-point Braun-Blanquet scale. Cover class values were then converted to percent covers using the mid-points of the scale ranges (Peet et al. 1998). We also measured plot water depths at the time of sampling each year.

To simplify analysis and presentation, we evaluated vegetation composition data for 2002 and 2004 to test the effects of planted grasses after the two initial years of drought, and then after two years of hydrologic recovery. We excluded from the data a few tree species (mainly sweetgum, *Liquidambar styraciflua* L., and oaks, *Quercus* spp.) that resprouted from small cut stumps after harvest, on the presumption that planted grasses could not influence such resprouting. For analysis, species were grouped into two functional classes by their wetland indicator category (Reed 1988), with obligate (OBL) and facultative wetland (FACW) species grouped as ''wetland'' species, and all facultative and upland categories (FAC, FACU, UPL) as ''non-wetland'' species. We chose this contrast because a restoration success criterion was to achieve a predominance of wetland plant species (De Steven et al. 2006); the two functional groups also provided consistent ecological data for comparing plots and wetlands. The vegetation variables analyzed were total species

Table 1. Annual mean (SE) wetland hydroperiod, late-summer plot water depth, and coverage attained by planted grasses in early August. Year 2000 is pre-restoration. n = 12 wetlands.

Year	Percent of year ponded†	Plot water depths in August (cm)	Percent cover of *Leersia*	Percent cover of *Panicum*
2000	7 (5)	0 (0)	—	—
2001	36 (7)	0 (0)	14 (4)	18 (4)
2002	16 (6)	0 (0)	27 (10)	37 (9)
2003	84 (4)	45 (6)	23 (7)	44 (10)
2004	46 (7)	0 (0)	41 (11)	66 (10)

† At the deepest central point; data from C. D. Barton, University of Kentucky.

richness and total percent cover (sum of all species covers), and richness and cover (sum of species covers) of each indicator group. For each variable, differences among the paired plot treatments (unplanted, *Leersia*, *Panicum*) were analyzed using a repeated-measures randomized blocks analysis of variance (ANOVA) model, with the 12 wetlands as blocks and the data for each year as a within-block repeated measure. To meet model assumptions, we applied square-root transformations to richness data and log transformations to cover data. Where the overall treatment effect was significant at $P \leq 0.05$, we used Dunnett's tests (Zar 1999) to compare each planted treatment to unplanted controls within years. Because some effects could develop in strength over time, we also noted tests with a significance level of $P \leq 0.10$. Wetland hydrologic variables were also analyzed with randomized blocks ANOVA models. Analyses were performed in SYSTAT 9 (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Hydrologic recovery was slowed by drought (Table 1), as hydroperiods during the first two years of restoration were significantly shorter than in the two subsequent years ($F_{3,\,33} = 85.0$, $P < 0.001$). In 2001, all wetlands were drying down by late April and remained mostly dry apart from transient ponding during some June rains; in 2002, all wetlands were dry for most of the year after early spring. In 2003, heavy rains resulted in prolonged ponding of all wetlands, with maximum spring water depths averaging 80 cm. By 2004, restored hydroperiods averaged 46% (Table 1), with a range of 20%–90%. The study plots were dry by late summer in all years except 2003. In that very wet year, plot depths averaged 45 cm and did not differ among plot treatments ($F_{2,21} = 0.2$, n.s.).

Despite the early drought, vegetative cover developed readily from the seed banks (see De Steven et al. 2006), and the planted grasses established in all wetlands in the first year. Across the study plots, a total of 103 plant species, all natives, was recorded in both 2002 and 2004, with an average of 26 species per wetland. Herbaceous species comprised 81% of all species and more than 90% of plot vegetative cover. In planted plots, cover of *Leersia* and *Panicum* increased from initial values of 1%–4% at planting to respective averages of 41% and 66% by the end of the fourth year (Table 1). There was a trend for the taller and stouter *Panicum* to develop somewhat higher cover more rapidly than the smaller *Leersia* ($F_{1,11} = 4.1$, $P < 0.10$). Cover of planted grasses generally reached values of 62%–90% by 2004; however, in a few wetlands the *Leersia* failed to exceed 15% cover after four years, whereas this occurred in only one planting of *Panicum*. Planted grass covers did not differ significantly between wetlands with longer (> 50%) or shorter (< 40%) 2004 hydroperiods ($t = 1.3$ and 1.9 for *Leersia* and *Panicum*, respectively, df = 10, n.s.).

By 2004, planted plots generally averaged fewer total species and fewer wetland (OBL, FACW) species than unplanted control plots ($F_{2,\,22} = 4.0$ and 6.5, respectively, both $P < 0.05$). The differences were significant in *Panicum* plots (Table 2), but weaker in *Leersia* plots because of the variable *Leersia* growth among wetlands. Differences in species number were not large, averaging 2–3 fewer species per plot where the grasses had been added. Planting had greater effects on the abundances (coverage) of wetland species. During the drought in 2002, cover of naturally colonizing wetland species averaged 22%–23% in all plot types (Table 2). With the added contributions of *Leersia* and *Panicum*, the planted plots had greater combined cover of all wetland species (averaging 49% and 59%, respectively) compared to controls ($F_{2,22} = 5.3$, $P < 0.05$). Consequently, planted plots attained higher total vegetative cover than controls during the drought (Table 2). After hydroperiods recovered by 2004, all plot types achieved approximately equal total cover (87%–100%). Cover of naturally recruited wetland species had increased to 54% in the control plots, but not in the planted plots (Table 2). However,

Table 2. Mean (SE) number of species and percent cover of wetland indicator groups in paired control and planted plots during drought (2002) and after hydrologic recovery (2004). Wetland species are OBL and FACW categories; non-wetland are FAC, FACU, and UPL categories (Reed 1988). Within each year, means in boldface differ from unplanted controls at $P < 0.05$; means in italics are differences at $P < 0.10$ (Dunnett's tests). n = 12 wetlands.

	2002			2004		
	Unplanted plots	*Leersia* plots	*Panicum* plots	Unplanted plots	*Leersia* plots	*Panicum* plots
Number of Species:						
Wetland species†	4.9 (0.6)	4.1 (0.4)	**3.0 (0.6)**	4.7 (0.7)	3.1 (0.5)	**2.8 (0.7)**
Non-wetland species	6.5 (1.2)	6.2 (1.1)	6.2 (1.1)	4.0 (1.0)	3.3 (1.0)	3.1 (0.9)
Total species†	11.4 (1.3)	10.2 (1.2)	*9.2 (1.4)*	8.7 (1.3)	6.4 (1.2)	**5.8 (1.5)**
% Vegetative Cover:						
Planted grass species	0	**27 (10)**	**37 (9)**	0	**41 (11)**	**66 (10)**
Other wetland species†	23 (8)	22 (10)	22 (11)	54 (12)	*24 (8)*	**13 (5)**
Non-wetland species	24 (7)	24 (6)	18 (6)	36 (15)	22 (11)	21 (10)
Total cover	48 (7)	**72 (10)**	**78 (13)**	90 (9)	87 (7)	100 (5)

† Not including the planted *Leersia* (in *Leersia* plots) or *Panicum* (in *Panicum* plots).

combined cover of all wetland species (planted plus other wetland species) still trended higher in planted plots (65% and 79% for *Leersia* and *Panicum* plots, respectively) than in unplanted controls (Dunnett's test significant for *Panicum*). Native wetland species whose cover was lower in planted plots included annuals and cespitose perennials favored by water drawdowns, such as warty panicgrass (*Panicum verrucosum* Muhl.), woolgrass (*Scirpus cyperinus* (L.) Kunth.), swamp smartweed (*Polygonum hydropiperoides* Michx.), and meadow-beauties (*Rhexia* spp.).

In contrast to their effects on wetland species, the planted grasses did not exhibit strong overall effects on non-wetland (facultative and upland) species (Table 2). Instead, between-year differences in hydrologic conditions were more important. Regardless of plot type, fewer non-wetland species were found in 2004 than in 2002 ($F_{1, 11} = 26.2$, $P < 0.01$), suggesting exclusion by higher water levels. Patterns for cover of non-wetland species were more complex. Non-wetland species cover was similar in all plot types in 2002 (18%–24%), but by 2004 it appeared that average non-wetland species cover had increased in unplanted plots (to 36%) even though the overall test was not significant (Table 2). Further analysis revealed that the apparent increase was attributable to six wetlands with shorter 2004 hydroperiods (ponded < 40% of the year), where non-wetland species cover in control plots increased significantly from 39% in 2002 to 69% in 2004 ($F_{1,5} = 20.9$, $P < 0.01$). In sites with longer 2004 hydroperiods (> 50% of the year), cover of non-wetland species decreased across all plot types, from an average of 18% in 2002 to 2% in 2004 ($F_{1,5} = 11.3$, $P < 0.05$). Non-wetland species whose 2004 cover was lower in planted plots were native ruderals such as dogfennel (*Eupatorium capillifolium* (Lam.) Small) and green-white sedge (*Carex albolutescens* Schw.).

In a few wetlands, plantings of *Leersia* attained only low levels of cover (< 15%), which may partially account for the weaker statistical effects in *Leersia* plots. Exploratory regression analyses (not shown) suggested a non-linear threshold effect, such that planted grass cover had to exceed approximately 30% to substantially influence the number or cover of other species.

DISCUSSION

Our first hypothesis, that planted grasses could facilitate community development, was supported. Compared to natural colonization alone, introducing these native rhizomatous grasses accelerated development of total vegetative cover and wetland species cover, notably during the initial drought conditions. As the planted grasses attained greater cover over time, they reduced local (plot-scale) richness and cover of other wetland species with more ephemeral life histories or non-clonal growth. Both *Leersia hexandra* and *Panicum hemitomon* are well-adapted to ponded conditions and can elongate their stems through deeper water (Kirkman and Sharitz 1993). This gives them a temporal growth advantage in the spring over species whose emergence must await seasonal water drawdowns. The planted grass coverages achieved in this study (62%–98% in successful plots) resemble those seen in natural herbaceous depressions in the region, where average cover of these matrix grasses ranges from

50%–90% (De Steven and Toner 2004). This relative cover dominance does not preclude a diverse flora in natural depressions, as other wetland species persist at lower abundances or emerge in open patches unoccupied by the dominant graminoids (Kirkman and Sharitz 1994).

Support for our second hypothesis, that planted grasses could suppress non-wetland species, was limited. Overall, the planted grasses did not appear to influence the presence and cover of non-wetland (facultative and upland) species, but this result was complicated by variation in restored hydrology. In general, development of wetter conditions by 2004 reduced the number of non-wetland species compared to the earlier drought period. However, there was weak evidence that the planted grasses might slow the development of non-wetland plant cover, but only where restored hydroperiods were too short to do so. Ability to suppress other species may develop with time as planted grasses develop full coverage. For example, well-established stands of robust graminoids such as *Panicum hemitomon* appear to reduce colonization by other plant species during drought periods (Mulhouse et al. 2005). An established dominant cover matrix could also potentially exclude exotic species (e.g., David 1999), although no exotic species colonized any of our study plots. In general, non-native species were rare in these restored depressional wetlands (De Steven et al. 2006); they appeared as occasional plants during the drought period and comprised less than 5% of more than 300 species found across all project wetlands. Non-natives were typically flooding-intolerant upland species not considered invasive in regional wetlands.

In the project wetlands overall (see De Steven et al. 2006), wetland plant species comprised 69% of all species in the remnant seed banks, which provided for adequate passive revegetation under varied hydrologic conditions. However, the resulting plant communities differed from those of natural herbaceous wetlands in lacking the typical clonal matrix species such as *Panicum* and *Leersia*. Thus, in depressional wetlands with adequate seed banks and hydrologic recovery, planting a full suite of species may not be needed to establish a successful restoration trajectory. Instead, selective planting of a few species could facilitate development of a more typical vegetative structure and offset potential deficiencies in seed bank composition.

Applications

This is the first published study to demonstrate the feasibility of transplanting these two species to facilitate restoration of depressional wetland vegetation. Our planting strategy was guided by findings from past literature on reintroducing wetland graminoids (e.g., Yetka and Galatowitsch 1999, Budelsky and Galatowitsch 2004). Key aspects to success were using plant material that could establish quickly, optimizing planting time within the seasonal growth cycle, and adjusting planting location to anticipate hydrologic conditions. Rooted tillers were transplanted in the spring, when shoots were emerging vigorously from overwintering rhizomes. We planted into saturated or very shallow-water positions at a time of falling water levels, which avoided the risk of deep inundation during the first critical growing season. The transient summer ponding during the first year may also have promoted successful grass establishment. Reasons for the low *Leersia* success in a few wetlands were uncertain, but may have included either shorter hydroperiods or overgrowth by woody vines whose occurrence was patchy within and among sites. Because *Leersia* is somewhat less drought-tolerant than *Panicum* (Kirkman and Sharitz 1993), it may be more sensitive to dry soil conditions when planted.

These two native grass species currently have limited to no commercial availability for use in depression wetland restorations. *Leersia hexandra* is typically found in depression ponds and may be uncommon elsewhere. It produces seed regularly, but little is known about propagating by this method. *Panicum hemitomon* is more widely distributed in depressional wetlands and in coastal freshwater marshes, but whether these habitats represent different ecotypes is unknown. Scant published information suggests that *P. hemitomon* may be used locally in coastal marsh restorations (Pezeshki et al. 2000, Mayence and Hester 2005). Its seed production is often poor, thus it generally must be propagated vegetatively. Our experiment demonstrated that rooted tiller-transplants could be outplanted successfully into depressional wetlands if spring conditions provide water or moist soils for establishment. The plants proved fairly tolerant of handling when the root systems were protected from desiccation. Both species established successfully across a range of restored hydroperiods. We planted in single large blocks to reduce edge effects in our experiment; however, where the goal is to supplement vegetation composition, an alternative strategy might be to plant tillers in dispersed clusters across the restoration site. If only small amounts of grass material were obtained from donor wetlands so that source populations were not depleted, the rhizomatous growth habit would allow rapid natural recovery of harvested patches. The donor materials obtained could be propagated in a nursery to increase quantities for outplanting.

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