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Plasticity in Bud Demography of a Rhizomatous Clonal Plant *Leymus chinensis* L. in Response to Soil Water Status

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We surveyed the bud demography of *Leymus chinensis* L. plants along a soil-moisture gradient that was caused by a flood in 1998 on the Song-nen Plain in northeastern China. The number of vegetative buds per ramet was influenced by soil water content, with regression curves being quadratic and the opening of the parabola pointing downward. In addition, the optimum regression models for the numbers of rhizomatous buds and tiller buds relative to soil water resulted in a quadratic parabola and exponential curve, respectively. Vegetative buds flourished between August and October, with plants producing more of those buds on flooded plots than on control sites. The number of rhizomatous buds per ramet was much higher than for tiller buds throughout most of the growing season, and production of the former was more apt to be affected by soil water status. This observed superiority of rhizomatous bud production was thought to be a consequence of the whole-plant adjustment that was stimulated by an abnormally high moisture content. It could also be interpreted as a strategy for "escape" from disadvantageous overly wet conditions. Moreover, the position-based preference for bud emergence along the ramets could be an underlying mechanism for selective ramet placement.

Keywords: bud, clonal plant, flooding, *Leymus chinensis*, plasticity, rhizome

Clonal growth is widespread throughout the plant kingdom and both productive and infertile habitats may be dominated by such species. Their clonal nature seems to be advantageous in colonizing and competing successfully in a range of environments (van Groenendael et al., 1996; de Kroon and Bobbink, 1997), with great potential for influencing community organization (Song et al., 2002). Because of their importance, the clonality of those plants has become a focus for study (Price and Marshall, 1999), including frequent examinations of the contributions of vegetative reproduction to population regeneration (Trenbath and Harper, 1973; Noble et al., 1979; Hartnett, 1990; Yang and Zhang, 1992; Soukopová, 1994; Verburg et al., 1996; Lenssen et al., 2000). In grasslands dominated by perennial species, the belowground reserves of the meristems or bud populations play a fundamental role in local population structure and dynamics (Benson et al., 2004). Because the vegetative buds can develop into new, potentially independent ramets, bud demography is of pivotal importance to population dynamics (Klimešová and Klimeš, 2003). The capacity to retain a reserve of buds or meristems for recovery from occasional damage is widespread among species (Vesk and Westoby, 2004). However the demography of vegetative buds in clonal plants, especially those that are rhizomatous herbs, has not received adequate attention (Klimeš et al., 1997).

Studies of morphological plasticity in clonal plants have analyzed responses to habitat quality in terms of spacer length and branching intensity. The ability of those parameters to respond to environmental quality has been interpreted as an expression of foraging behavior because it represents the potential to intensify the placement of ramets in more favorable microhabitats (e.g., patches) within a heterogeneous environment (de Kroon and Hutchings, 1995). In plants, foraging may be achieved through the morphological responses of shoots, rhizomes, stolons, or roots to patchy resources; in a broader sense, many types of responses can be considered foraging (de Kroon and Hutchings, 1995). One widely recognized means in clonal plants is via morphological plasticity in their ramet placement in response to those patches (Humphrey and Pyke, 1997). Spreading stoloniferous or rhizomatous plants have the capacity to selectively place ramets in benign patches and to escape from adverse ones by means of plasticity in their internode lengths and branching frequency (see van Kleunen and Fischer, 2001). However, another mechanism for selective placement has so far been either completely ignored or not recognized as such. Namely, the ratio of rhizomatous buds to tiller buds, which grow out from different positions on the clonal ramets, can be adjusted, thus altering the vegetative spread of the entire clone. Tiller buds (TBs) can only develop in the shoot bases of the mother ramets, so that the population distribution cannot be extended as effectively as by rhizomatous buds (RBs), which grow on the nodes of rhizomes. Thus, a rhizomatous clonal plant will spread its population in terms of a distribution that is based more on RBs than on TBs, so that RBs contribute more to population expansion. For example, we might hypothesize here that, in adverse habitats (heavily flooded sites), plants will produce more RBs to effectively escape and forage more favorable conditions.

Unfortunately, most previous studies of bud banks have emphasized bud density and have neglected the corresponding variations in aboveground shoot density. Such a correlation should be positive because the stand with

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denser shoots should have more photosynthetic accumulation than the sparser site, enabling plants growing on the former to store much more nutritious matter for supplying VB (vegetative bud) production. In reality, however, this principle is somewhat limited because, if the ramets are too densely distributed, the supply of nutrients for VB production is reduced due to inter-ramet competition. Therefore, Hendrickson and Briske (1997) have focused their research on the contribution of shoot density to bud density.

Flooding that occurred on the Song-nen Plain of northeastern China in late August, 1998, provided the soil-water gradient for this study. Our objective was to investigate any correlations between the VB-producing capacity of a clonal species, *Leymus chinensis*, and moisture conditions in order to clarify the impacts of flooding disturbances. We also examined foraging behavior of plants escaping an adverse habitat. This could be reflected in the adjustment of the ratio of RBs to TBs, which would then represent the plasticity of the bud bank.

MATERIALS AND METHODS

Species Description

As a typical perennial rhizomatous grass and a dominant landscape plant on the Song-nen Plain, *Leymus chinensis* (Trin.) Tzvel. (Gramineae) depends mainly on clonal growth to maintain its role within communities (Yang et al., 1995). This species is distributed in the eastern region of the Eurasian Steppe zone, which includes the outer Baikal area of Russia, the northern and eastern parts of the People's Republic of Mongolia, the Northeast China Plain, the Northern China Plain, and the Inner Mongolia Plateau of China. Plants are highly tolerant of drought, low fertility, and high pH, and they produce high yields of biomass. This makes crops very palatable to grazing livestock and useful as hay (Zhu et al., 1981). Its highly branched rhizomes lie horizontally about 10 cm beneath the surface. These rhizomes have long internodes between ramets, giving rise to extensively spreading clones. The bud bank of a *L. chinensis* population comprises two types of vegetative buds -- rhizomatous and tiller -- the former developing from the nodes and apices of the rhizomes, the latter, from tiller nodes.

Site Description

Our study area is located in the Sanjiadian National Pasture of Da'an, Jilin Province, in northeastern China (45°25′~45°30′N, 124°10′~124°21′E). The climate in this

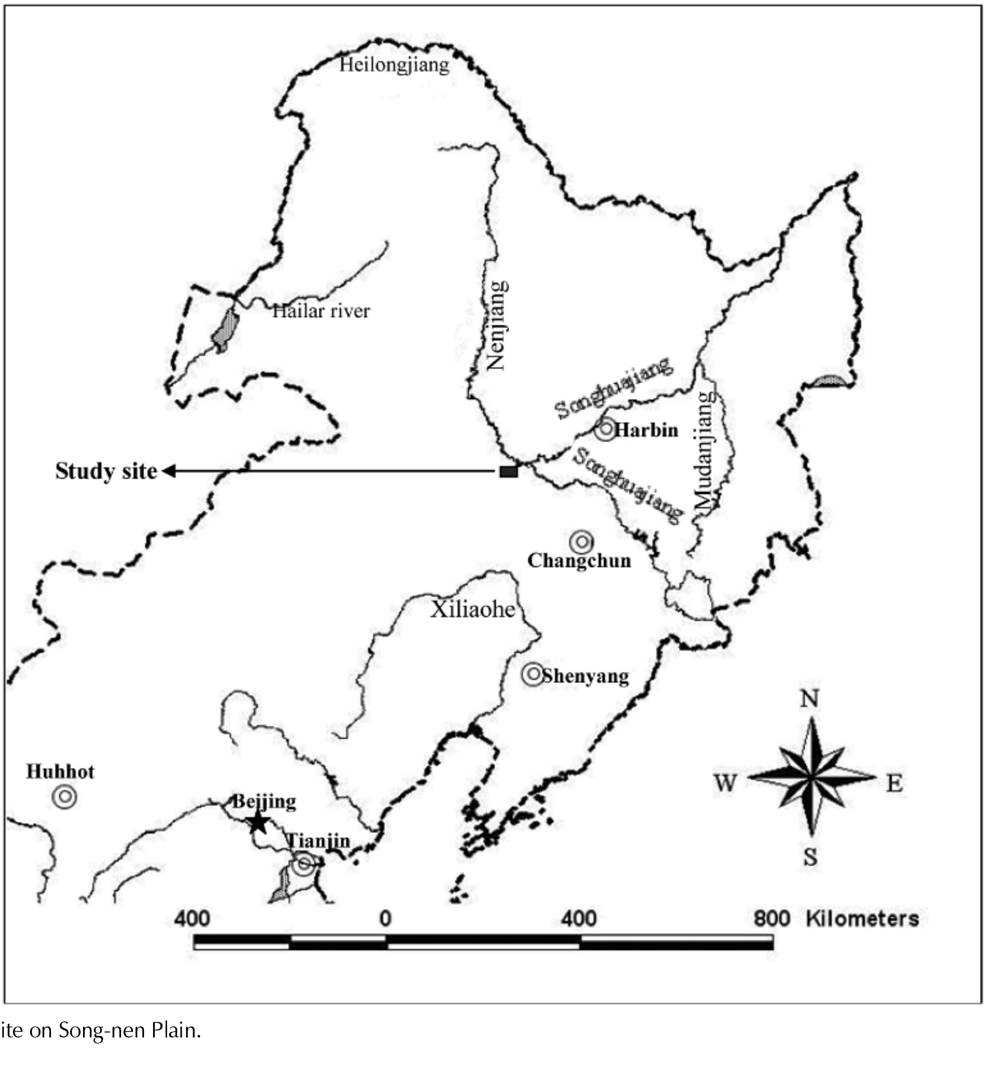

Figure 1. Study site on Song-nen Plain.

warm temperate zone is of a semi-arid and semi-humid monsoon type, characterized by typical continental climatic features. In 1998, precipitation totaled 411 mm, and the average annual atmospheric temperature was 4.3, based on data from the Da'an Meteorological Observation Station. Being very close to the junction of the Nenjiang and Songhuajiang Rivers (Fig. 1), this region belongs to a low floodplain in the southern part of the Song-nen Plain, which was formed by an alluvial flood area and low steppe land that is flat, with only slight topographical undulations. Most of the soil has been secondarily salinized because of overgrazing and subsequent vegetative degradation. Before the 1998 flood, the slope had an almost uniform soil type, and vegetation was mainly in the *L. chinensis*-dominated community.

Flooding Gradient and Experimental Plots

The study site was located on a mild slope (inclination <5°) that was subject to different flooding histories. At higher elevations, events were shorter in duration, while at the lower elevations, sites had undergone longer periods of inundation. Thus, a natural flooding gradient had formed, which enabled us to compare the effects of varying flooding disturbances on grassland vegetation.

To compare the effects of different flooding intensities on VB-producing capacity, we selected four rectangular plots, coded T_0, T_1, T_2, and T_3, along this gradient. Each of these 100 m×20 m plots was nearly parallel to all others, and their longer sides were approximately perpendicular to the direction of water flow. By elevation, the plots were ordered as $T_0>T_1>T_2>T_3$, with T_0 serving as our control because it was the highest and the only one left unflooded. The others were subjected to flooding of different durations, i.e., 3 (T_1), 5 (T_2), and 7 (T_3) months. Each of the neighboring flooded plots were 0.3~0.5 km apart, while the T_0 (unflooded) was about 1 km from the nearest flooded plot (T_1).

Sampling Methods

From May to October of 1999, ramets of *L. chinensis* were sampled every 15~20 d, using a non-quadrat multiple-site sampling method. On every date, more than five points (50 ramets per point) were sampled in each plot, so that >250 ramets were examined in each plot at any given time. To sample, all aboveground plant parts and belowground rhizomes were carefully dug out to maintain the inherent links among rhizomes, aboveground organs, and all VBs for ease of identification. After the rhizomes were rinsed of their soil, we classified and counted the RBs (on the nodes and ends of rhizomes), TBs (developing from the tiller nodes), and spring tillers (developed from the buds that emerged in the current year). Those spring tillers were usually tender, small, and weak compared with the winter tillers, which developed from buds that had emerged in the previous Fall.

Data Analyses

The mean number of VBs per ramet served as the index for describing the ability of plant populations to produce those buds. This improved index was used to analyze the relationships between VB-producing capacity in *L. chinensis* and soil water status.

Ratios of VB, RB, and TB counts in August to their corresponding tiller numbers were considered indices of the capacities for *L. chinensis* populations to produce VBs, RBs, and TBs respectively. These data were regressed with corresponding soil water contents, and the regression models were diagrammed with Sigma Plot 8.0. The ratios of VB numbers to corresponding tiller numbers from May to October were used to diagram the seasonal dynamics of VB production without distinction for RBs and TBs. Ratios of RB and TB counts to corresponding tiller counts from August to October, the most prolific period for VB production, began to differentiate among plots, and were used to diagram the monthly dynamics of RB and TB production.

RESULTS

Correlations Between VB Production and Soil Water Status

The mean number of VBs per tiller was closely related to soil water conditions (Fig. 2a). Our regression model displayed a quadratic parabola that opened downward, indicating that the capacity of *Leymus chinensis* to produce VBs was highest under a medium soil water content, 19.66%. Therefore, we inferred that mild flooding raised soil moisture levels, thus promoting the VB-producing capacity by those populations. In contrast, intense flooding disturbances meant that soils were too wet or waterlogged, which led to anoxia of the root systems, impeded respiration, slower metabolism, and an ultimate decline in VB-producing capacity.

When soil water content increased, the mean number of TBs per tiller decreased exponentially (Fig. 2b). All points on the curve corresponded to values of <1 on the vertical axis, which indicated that, under those conditions, TBs were fewer than the number of parent tillers. However, the regression curve for mean RB number per tiller to soil water content displayed a quadratic parabola opening downward (Fig. 2c). A peak value of 1.97 corresponded to a soil water content of 19.86%; values on the vertical axis for all points on the curve ranged from 1 to 2. Therefore, we concluded that the capacity for vegetative propagation by the rhizomes was much higher than that by the tillers under the soil water conditions examined here.

Differentiation of Temporal Dynamics for VB Production in Response to Varying Flooding Regimes

VB production flourished from August~October compared with only a slow increase seen from May to late July. Although we noted little discrepancy in those dynamic alterations among the four plots during that period, from early August, significant differences began to emerge and widen. This was especially noticeable on the three flooded plots, whereas changes on the control plot became apparent more slowly (Fig. 3a).

The dynamic curve for RB-producing capacity showed that Plots T_2 and T_3 were very similar in their changes for that parameter while Plot T_1 differed slightly (Fig. 3b). For example, from August to October, capacities on Plots T_2 and

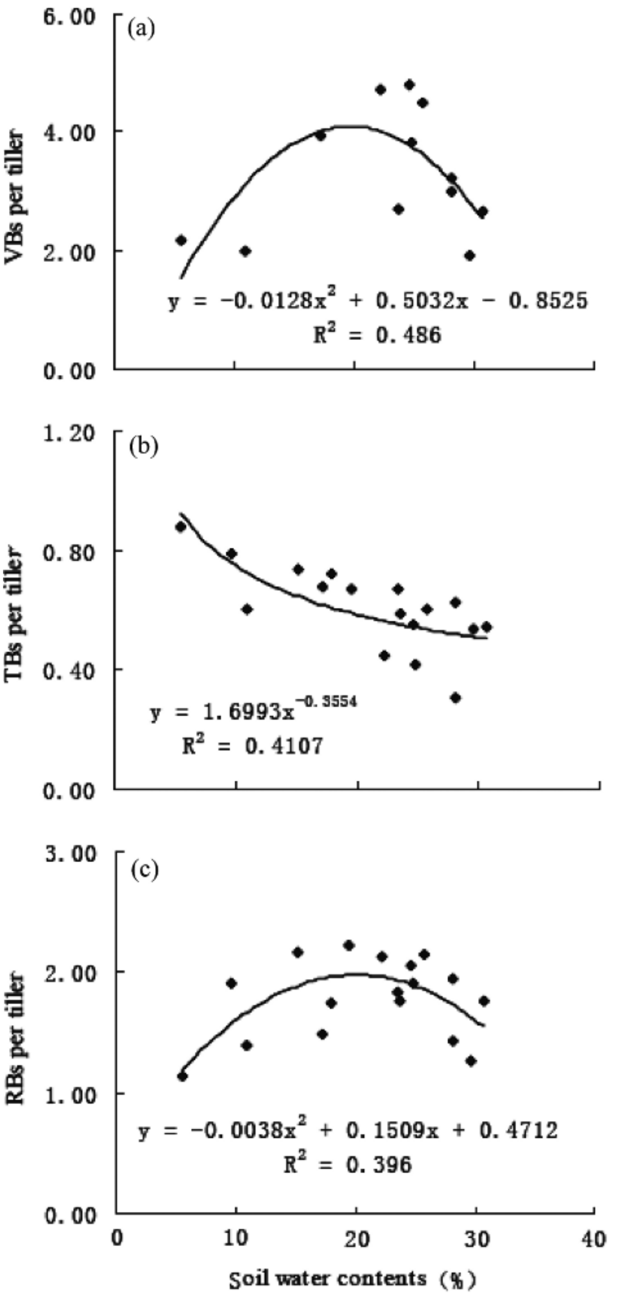

Figure 2. Responses to soil water status as reflected in production of total vegetative buds (**a**), rhizomatous buds (**b**), and tiller buds (**c**) from *Leymus chinensis*.

T_3 first declined and then increased, as manifested by the wide-opened "V"-shaped curve. In contrast, the RB capacity on Plot T_1 showed an essentially linear increase throughout that period. The main difference occurred from early August to mid-September, when capacities of Plots T_2 and T_3 were diminished while that of Plot T_1 was improved. We inferred that this difference was probably related to the output dynamics of VBs, which rose continuously from early August to mid-September when it reached its peak value (Fig. 3d). Moreover, the majority of VB output led to RB output, and *L. chinensis* populations on Plots T_2 and T_3 could not produce enough RBs to compensate for this because soil water contents were too high, thereby leading to a decline in the ratio of RB numbers to total tillers. In comparison, Plot T_1 had endured only 3 months of flooding the year before, after which it experienced 8~9 months of more normal transpiration and evaporation, such that its soil conditions were fairly suitable for RB production. This status not only compensated for but also exceeded the previously reduced production of rhizomes, resulting in a continuous increase in that RB:total tillers ratio.

Trajectories for the dynamic changes in TB production by *L. chinensis* populations on the three flooded plots appeared similar, rising from early to late August, then declining until mid-September, when they again rose steeply through late October. Nearly a completely opposite trend was observed for the control plot, T_0, during all three time periods (Figure 3c). On the flooded plots, the decline from late August to mid-September may also have been related to the output dynamics of VBs. In fact, the percent output of VBs on T_1, T_2, and T_3 increased quite abruptly, and *L. chinensis* populations could not produce sufficient TBs to compensate, a phenomenon that led to a decline in the ratio of TB numbers to total tiller numbers. In contrast, changes in VB output on the control plot were comparatively stable and slow, and TB production was less affected by soil conditions so that the number of tiller buds continued increasing during that period of observation. Only from mid-September on did TB production on the control plot begin to decline, probably as a result of extremely dry soil.

DISCUSSION

We propose that the VB-producing capacity of *Leymus chinensis* populations is first determined by inherent developmental rhythms in those plants. This has been demonstrated by Watson et al. (1997). Moreover, we suggest that soil water status is a factor that influences bud production. Mild flooding can elevate moisture content, which then enhances the capacity to produce VBs. Intense flooding, however, can cause soils to be too wet or, even, waterlogged. This leads to anoxia, slower rates of respiration and metabolism, and lower VB-producing capacity (Blom and Voesenek, 1996).

At our study site, the capacity for vegetative propagation was much higher for rhizomes than for tillers, a finding that conflicts with results reported by Yang and Li (1996). This difference may have occurred because our research was conducted over a soil water gradient, whereas that previous study did not include such an experimental gradient, and because that earlier site was in an arid location that was not conducive to the vegetative propagation of rhizomes or the abundant production of RBs.

VB production by our *L. chinensis* populations was closely related to soil water conditions, and was absolutely affected by that flooding event the previous year. In contrast, measured precipitation was much lower in 1999, and our control plot had not been influenced by the 1998 flooding, making it much drier than on the three disturbed plots during our study period. Therefore, we hypothesized that this was the main factor controlling the vegetative propagation of *L. chinensis* populations there. Nevertheless, those three dis-

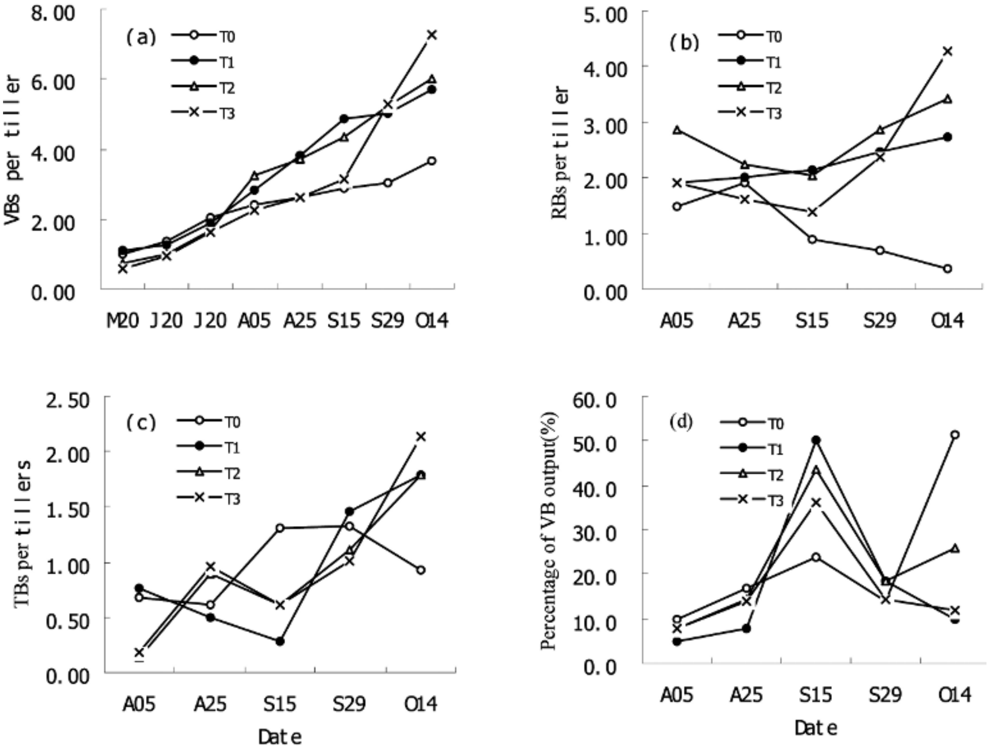

Figure 3. Temporal dynamics of vegetative bud, VB (**a**), rhizomatous bud, RB (**b**), and tiller bud TB (**c**) production; and VB output (**d**) from *Leymus chinensis* within plots subjected to different flooding regimes.

turbed plots were still somewhat wet even in that dry year of 1999, a result of their exposure to flooding in 1998. Such high soil water contents induced greater VB production (relative to the control plot) from August~October. During that time, the impact of earlier flooding was much more obvious than had been observed from May~July. With regard to rhizomatous- and tiller-bud production, which was more susceptible to soil water conditions, success depended mainly on physical positioning for their development. That is, TBs grew on the tiller nodes, and their survival relied more on the parent plants compared with RBs, which formed on rhizomes that were located rather distant from the parent tissue.

The phenomenon that *L. chinensis* populations produces many more RBs than TBs, especially under conditions of high soil water content (or, usually, flooding) might be attributed to the great need by that species to seek more suitable habitats for its survival and reproduction. However, this interpretation implies an apparent result rather than one that is substantive or mechanistic. What might underlie this is that the rhizomes are generally not well adapted to such an inundated environment, but the plant as a whole must extend those rhizomes and produce more buds in order to reach a drier or better habitat. Likewise, TBs can develop only *in situ* and that alone is not sufficient for increasing this population as effectively as via RBs. This might be considered an indicator of behavior in foraging for light, water, and nutrients. Thus, under unfavorable environmental conditions, plants may invoke plasticity to help escape such adversity (de Kroon and Schieving, 1990; Hutchings and de Kroon, 1994). The underlying mechanism for this behavior is probably an adjustment in the ratio of TBs to RBs. Although the viable bud bank contributes to the extent of plant foraging in response to habitat (de Kroon and Schieving, 1990), these modifications by different plant organs have not previously been reported. Therefore, this very challenging situation is a problem that should continue to be studied, especially with indoor experiments.

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