Growth responses of the intertidal seagrass *Zostera japonica* to manipulated sea level rise conditions

**Seung Hyeon Kim**  
**Jae Woo Kim**  
**Young Kyun Kim**  
**Kun-Seop Lee** *

ABSTRACT.—Although most seagrasses inhabit subtidal areas, a few species occur in the intertidal zone. The seagrass, *Zostera japonica* Asch. & Graebn., is an intertidal seagrass species, and thus this species may be vulnerable to environmental changes associated with sea level rise due to climate change. We examined the effects of continuous submergence conditions, which might be caused by sea level rise, on the growth of the intertidal seagrass, *Z. japonica*. In the present study, submerged conditions were generated in a *Z. japonica* meadow in the intertidal zone using transparent cylindrical cores, and the growth responses to the inundation conditions were examined. Daily photon flux density and temperature were not significantly different between the manipulated submerged and the control intertidal conditions during the experimental period. Increases in shoot height, biomass, and leaf productivity were among the acclimatory responses of *Z. japonica* to the inundation conditions. Shoot density, however, decreased rapidly in the submerged conditions as a result of the self-shading induced by taller and larger shoot sizes. Thus, prolonged inundation, which would be induced by a rise in sea level, had both positive and negative effects on the growth of the intertidal seagrass, *Z. japonica*, which exhibited plasticity at the individual and population levels. According to the results of our study, the restricted distribution of *Z. japonica* in the intertidal zone may not be a consequence of tidal inundation stress in the subtidal zone.

Seagrasses are a distinct group of flowering plants that evolved from terrestrial angiosperms and returned to the sea approximately 100 Ma (den Hartog 1970, Les et al. 1997, Waycott et al. 2006). Seagrasses have adapted to living completely submerged in saline environments (Olsen et al. 2016), and play critical roles in coastal and estuarine ecosystems (Duffy 2006, Acosta et al. 2007, Duarte et al. 2010). Although most seagrass species inhabit the subtidal zone of estuarine and coastal ecosystems, a few species have a physiological tolerance to air exposure during low tide and can grow in the intertidal zone (Beer et al. 2006, Shafer et al. 2007, Cabaço et al. 2009).
Intertidal seagrasses are exposed to both submergence and emersion due to tidal changes. Because seagrasses growing in the intertidal zone are periodically exposed to air during low tide, they undergo extreme temperatures, high photo-inhibitory irradiance, and desiccation stress compared with seagrasses in the subtidal zone (Leuschner et al. 1998, Koch 2001).

*Zostera japonica* Asch. & Graebn. originated from subtropical and temperate regions of the northwestern Pacific coast and was introduced to the eastern Pacific coast in the early 20th century, along with oyster stocks imported from the western Pacific coast (Harrison and Bigley 1982, Short et al. 2007). Because *Z. japonica* usually occurs in mid- to upper intertidal zones, it is considered to be an intertidal seagrass species (Britton-Simmons et al. 2010, Shafer et al. 2014, Kim et al. 2016). *Zostera japonica* consists of monotypic or mixed meadows, with subtropical or temperate species such as *Halophila ovalis* (R. Brown) Hook.f., *Halodule uninervis* (Forsskål) Asch., *Halophila beccarii* Asch., and *Zostera marina* L. (Huang et al. 2006, Shafer et al. 2007, Kim et al. 2016). On the Pacific coast of North America, *Z. japonica* displays distinct vertical zonation patterns, including disjunct, overlapping, and mosaic overlapping zonations with *Z. marina*, which occupies the lower intertidal to subtidal zones (Shafer et al. 2014). In the eastern Pacific region, many studies have been conducted on the distributional range, distinct vertical zonation, and eco-physiological characteristics of *Z. japonica* to better understand and manage this introduced seagrass species (Harrison and Bigley 1982, Shafer et al. 2007, 2011, 2014, Young et al. 2008, Britton-Simmons et al. 2010, Kaldy et al. 2015). In its native range on the western Pacific coast, *Z. japonica* beds are frequently exposed to various natural and anthropogenic disturbances, and bed coverage is declining gradually (Park et al. 2011, Zhang et al. 2014). There have been relatively fewer studies on the ecology and physiology of *Z. japonica* conducted in its native range than in its introduced areas on the eastern Pacific coast (Lee et al. 2005, Choi et al. 2016, Kim et al. 2016).

The global sea surface temperature has risen in the past century by 0.4–0.8 °C and is predicted to increase further during the coming decades (IPCC 2001, 2013). As a result of warming seawater leading to thermal expansion of the oceans, coupled with run-off from ice-melt, sea level is rising at approximately 2 mm yr\(^{-1}\) (IPCC 2001). A rise in sea level will increase water depth and reduce light availability in coastal locations, and thus alter the distribution and function of ecologically and economically important marine ecosystems, such as seagrass meadows, mangrove swamps, coral reefs, and saltmarshes (Hoegh-Guldberg and Bruno 2010, Saunders et al. 2013, Short et al. 2016). Intertidal seagrasses may encounter more frequent submerged conditions as a result of sea level rise in the future. Thus, sea level rise may be a challenge to organisms inhabiting the intertidal zones, and a key factor determining the ecological and physiological characteristics and distribution of intertidal seagrass such as *Z. japonica*.

The factors regulating the growth and distribution of intertidal seagrasses vary along the vertical gradient of the intertidal zone (Cabaço et al. 2009, Kim et al. 2016). The growth of intertidal seagrasses in the lower intertidal zone is affected by tidal inundation, light availability, competition with subtidal species, and physical disturbances caused by tidal currents, whereas growth in the upper intertidal zone is influenced by desiccation stress (Koch 2001, Boese et al. 2005, Cabaço et al. 2009, van der Heide et al. 2010, Kim et al. 2016). Thus, we examined the effects of continuous submergence, which might be caused by a rise in sea level, on the growth of the
intertidal seagrass, *Z. japonica*. We created submerged conditions in a *Z. japonica* bed in the intertidal zone using cylindrical plexiglass cores, and then compared the growth of *Z. japonica* between the manipulated submerged and the control intertidal conditions. The present study provides valuable insight into the possible fate of the intertidal seagrass *Z. japonica* under the disturbances associated with sea level rise caused by global climate change.

**Materials and Methods**

**Study Site.**—The study site was located in Koje Bay (34°48′N, 128°35′E) on the southern coast of Korea (Fig. 1). Three *Zostera* species, *Z. japonica*, *Z. marina*, and *Zostera caespitosa* Miki, were distributed sequentially from the intertidal zone to a water depth of approximately 5 m relative to the mean lower low water. The study site was characterized by a high sand content in sediments, and the tidal regime was semi-diurnal, with a tidal range of approximately 2.5 m (Tide Tables for the Coasts of Korea, Korea Hydrographic and Oceanographic Administration; http://www.khoa.go.kr). *Zostera japonica* is distributed in the intertidal zone and regularly exposed to air for approximately 1–4 hrs daily during low tide. Because the growth of *Z. japonica* varies significantly along the vertical gradient in the intertidal zone (Kim et al. 2016), our study was conducted at an intermediate location of the intertidal zone in a monospecific meadow of *Z. japonica*.

**Manipulation of the Submerged Conditions.**—The submerged conditions were manipulated using a plexiglass cylinder in the intertidal *Z. japonica* meadow (Fig. 1). Five replicate transparent plexiglass cores (50 cm diameter; 1 m height) were inserted to a sediment depth of approximately 70 cm to prevent seawater leakage from the inside of the cores. Thus, approximately the top 30 cm of the plexiglass core...
was located above the sediments, and submerged conditions were created during low tide in the intertidal *Z. japonica* bed. Approximately 10–15 cm water were consistently retained inside the cylindrical cores during low tide (Fig. 1). Five replicate transparent cylindrical cores with drainage holes at ground level were also deployed on the *Z. japonica* bed as controls (Fig. 1). All cores were deployed at the same tidal level and were at least 1 m away from each other.

**Environmental Parameters.**—Photon flux density (PFD; μmol photons m$^{-2}$ s$^{-1}$) was monitored every 15 min using an Odyssey photosynthetic irradiance recording system (Dataflow Systems, Christchurch, New Zealand) in both the manipulated submerged and control cores from July to November 2009. The Odyssey sensor was regularly cleaned to minimize fouling by epiphytes and sediments. The logger was calibrated using a LI-1400 data logger and LI-193SA spherical quantum sensor (Li-Cor, Lincoln, NE, USA). Daily PFD (mol photons m$^{-2}$ d$^{-1}$) was calculated as the sum of the quantum flux over a 24-hr period. Water temperature was measured every 15 min from July to November 2009 using the Hobo StowAway Tidbit® temperature data logger (Onset Computer Corp., Bourne, MA), and the daily average water temperatures were calculated. Because the sensors used for the PFD and temperature measurements were placed at the seagrass canopy level, in the control cores, air temperature and surface irradiance were logged when the sensors were exposed to the air during low tide, whereas water temperature and underwater irradiance were measured during inundated conditions. In the manipulated submerged conditions, water temperature and underwater irradiance were logged over an entire day.

**Biological Measurements.**—Shoot density, morphology, biomass, and leaf productivity of *Z. japonica* were measured biweekly or monthly in the manipulated submerged and control cores and the adjacent natural meadow (reference site) from July to November 2009. The reference site was surveyed to determine the effects of the experimental cores on seagrass growth during the experimental periods. The number of shoots within a permanent quadrat (10 × 10 cm), which was deployed in each core and the reference site, was counted to estimate shoot density. Because the initial shoot density was slightly different in each core, the relative shoot density was expressed as a percentage of the initial shoot density. Four to five mature *Z. japonica* shoots were haphazardly collected from each core and the natural reference meadow to measure the individual shoot weight and shoot morphological characteristics, such as shoot height, sheath length, and leaf width. To estimate individual shoot weight, the shoots were thoroughly cleaned of epiphytes and sediments using tap water, separated into above- and below-ground tissues, and then dried at 60 °C to constant weight. Above-ground and below-ground biomasses (g dry weight m$^{-2}$) were estimated by multiplying the weights of the above- and below-ground tissues by the shoot density.

Leaf productivity per shoot was estimated using a modified blade marking technique (Zieman 1974, Kentula and McIntire 1986, Kowalski et al. 2009). A quadrat (5 × 5 cm) was haphazardly placed in each core and the reference site, and all shoots within the quadrat were pierced through the sheath using a fine acupuncture needle (0.15 mm in diameter). After approximately 2–4 wks, the marked shoots were retrieved, and leaf materials were divided into leaf tissues produced before and after marking. The newly produced leaf tissues were dried at 60 °C to constant weight. Leaf productivity per shoot (mg dry weight shoot$^{-1}$ d$^{-1}$) was calculated by dividing
the dry weight of newly produced leaf tissues by the duration of marking. Areal leaf productivity (g dry weight m⁻² d⁻¹) was calculated by multiplying the leaf productivity per shoot by the shoot density. The leaf elongation rate (cm shoot⁻¹ d⁻¹) was also estimated by dividing the length of new leaf tissues by the duration of marking.

Statistical Analyses.—All values were reported as means with standard error. Statistical analyses were performed using SPSS 23.0 (SPSS Inc., Chicago, IL). Data were tested for normality and homogeneity of variance to meet the assumptions of parametric statistics. If these assumptions were violated, the data were square root-transformed. Significant differences in irradiance, water temperature, shoot density, biomass, morphology, and productivity among treatments (the submerged cores, control cores, and the reference meadow) and among sampling times were determined by two-way analysis of variance (ANOVA). When a significant difference (α = 0.05) was detected by ANOVA, the means were analyzed using the Student-Newman-Keuls (SNK) test to determine where they occurred. During post hoc means comparison testing, we made no Bonferroni-type corrections to control for inflation of Type I error.

Results

Irradiance and Temperature.—Daily PFDs did not differ significantly between the manipulated submerged and control cores (12.6 and 14.2 mol photons m⁻² d⁻¹, respectively) during the experimental periods (ANOVA: $F_{1, 248} = 1.367$, $P = 0.243$) (Fig. 2A). The average daily PFD was significantly higher during July–August than September–November in both the submerged and control cores (SNK test: $P$
Temperature also did not differ significantly between the submerged and control cores (ANOVA: $F_{1, 252} = 2.187, P = 0.140$), with average values of 20.8 and 20.5 °C, respectively (Fig. 2B). Temperature was highest (27.7 °C) in August and lowest (11.0 °C) in November.

SHOOT DENSITY AND MORPHOLOGICAL CHARACTERISTICS.—Relative shoot density, as a percentage of the initial density, was not significantly different among the submerged cores, control cores, and the reference meadow until September (ANOVA: $F_{2, 54} = 0.241, P = 0.787$), i.e., 2 mo after submergence treatment (Fig. 3). However, relative shoot density decreased more rapidly in the manipulated submerged cores than in the control cores and the reference meadow after 2 mo of submergence treatment (Fig. 3). Shoot densities decreased to approximately 17% and 41.3% of the initial shoot density in the manipulated submerged and control cores, respectively, at the end of the experiment (Fig. 3). Shoot density in the reference meadow was much higher than those in both the submerged and control cores, and was decreased to 63.6% of the initial shoot density by the end of the experiment (Fig. 3).

Shoot height and sheath length were significantly different among the submerged cores, control cores, and the reference meadow (ANOVA: $F_{2, 419} = 26.966$ and $F_{2, 419} = 29.750$, respectively; both $P < 0.001$) (Fig. 4A, B). Shoot height and sheath length were approximately 1.5-fold greater in the submerged cores than in the control cores after 2 mo of the experiment, but were similar in November (Fig. 4A, B). Leaf width differed significantly among the submerged cores, control cores, and the reference meadow (ANOVA: $F_{2, 419} = 3.908, P < 0.05$) (Fig. 4C). Shoot height, sheath length, and leaf width increased until September, after which they decreased through the end of the experiment in all treatments, with the exception of sheath length in the control cores (Fig. 4A–C). The weights of the above- and below-ground and total tissues of individual shoots were significantly different among the submerged and control cores and the reference meadow (ANOVA: $F_{2, 419} = 55.100$, $F_{2, 419} = 30.580$, and $F_{2, 419} = 57.287$, respectively; all $P < 0.001$) (Fig. 4D–F). The weights of individual shoots were
approximately 2-fold higher in the submerged cores than in the control cores during September and October, 2–3 mo after submergence treatment.

Biomass and Leaf Productivity.—Above- and below-ground and total biomasses were significantly different among the submerged cores, control cores, and the reference meadow (ANOVA: $F_{2,72} = 24.363$, $F_{2,72} = 25.073$, and $F_{2,72} = 24.805$, respectively; all $P < 0.001$), and they varied significantly with sampling time (ANOVA: $F_{6,72} = 36.993$, $F_{6,72} = 25.889$, and $F_{6,72} = 31.402$, respectively; all $P < 0.001$) (Fig. 5). Mean above- and below-ground and total biomasses were much higher in the submerged cores than in the control cores (Fig. 5). The effects of the submergence treatment on above- and below-ground and total biomasses were distinct in September, approximately 2 mo after initiation of the submergence treatment. Maximum total biomass was significantly higher in the submerged cores (461.1 g dry weight m$^{-2}$)
than in the reference meadow (353.0 g dry weight m⁻²) and the control cores (209.1 g dry weight m⁻²) (SNK test: \( P < 0.001 \)).

Leaf productivity per shoot was not significantly different among the submerged cores, control cores, and the reference meadow during the first 2 months (July and August) of the experiment (SNK test: \( P = 0.148 \)), but was significantly higher in the submerged cores than in the control cores after 2 mo of submergence treatment (\( P < 0.05 \)) (Fig. 6A). Areal leaf productivity was also significantly higher in the submerged cores than in the control cores in September (SNK test: \( P < 0.05 \)), i.e., after 2 mo of submergence treatment; however, during the later periods, there was no significant difference between the submerged and control cores (\( P = 0.0626 \)) (Fig. 6B). The leaf elongation rate also displayed a similar trend to leaf productivity (Fig. 6C).
Seagrasses can grow under a wide range of environmental conditions in intertidal and subtidal regions because of their plasticity at the physiological, individual, and population levels (Cabaço et al. 2009, Park et al. 2016). Considerable morphological variability in seagrasses has been reported along the vertical gradient in intertidal and subtidal zones (Yabe et al. 1996, Tanaka and Nakaoka 2004, Boese et al. 2005, Park et al. 2016). Significant declines of productivity and above-ground biomass coupled with shorter leaves due to longer exposure time has been reported for seagrass species in the intertidal zones (Tanaka and Nakaoka 2004, Park et al. 2016, Suonan et al. 2017). Seagrasses in shaded regions or increasing water depth conditions tend
to invest a higher proportion of their energy toward leaf formation and thus produce longer leaves or stems extending toward the water surface for more light acquisition (Krause-Jensen et al. 2000, Boström et al. 2004, de los Santos et al. 2010). *Zostera japonica* plants in the present study responded to the manipulated submerged conditions by increasing their leaf length. An increased above-ground tissue biomass coupled with longer leaves was also observed after the submergence treatment. The manipulated submerged conditions in the present study, which reduced desiccation stress, likely provided more favorable conditions for the growth of *Z. japonica* leaf tissues, and consequently led to increases in leaf size and above-ground biomass.

In subtidal seagrass species, increased leaf tissue biomass in deeper water is caused by a greater biomass allocation to above-ground tissues, consequently leading to an increase in the above- to below-ground biomass ratio (Krause-Jensen et al. 2000, Olesen et al. 2002, Collier et al. 2007). This increase in the above- to below-ground ratio is considered to be advantageous for adapting to low light availability, because non-photosynthetic below-ground tissues act as a respiratory burden (Olesen et al. 2002, Collier et al. 2007). However, in contrast to subtidal seagrasses, both the above- and below-ground tissue biomasses of the intertidal seagrass *Z. japonica* in our study increased at the same rate in the manipulated submerged conditions; thus, the increased leaf biomass in submerged conditions was not caused by increased biomass allocation to above-ground tissues. Consequently, the above- to below-ground biomass ratio in the manipulated submerged conditions was almost the same as that in the control intertidal condition in the present study, with average ratios of 2.3 and 2.4, respectively. In the intertidal seagrasses *Zostera noltii* Hornem. and *Z. japonica*, longer and thicker rhizomes accompanied by a greater shoot height has been observed in the lower intertidal zone, in which the intertidal seagrass plants are submerged more frequently, compared with in the upper intertidal zone (Cabaço et al. 2009, Kim et al. 2016). The increase in below-ground tissues in the submerged conditions appeared to be an adaptive response of the intertidal seagrass, to provide a firm anchoring to larger shoots in the submerged conditions.

In addition to morphological plasticity, changes in shoot density along the vertical gradient in intertidal and subtidal zones have also been suggested to be an adaptive response of seagrasses to light availability and competitive interactions (Cabaço et al. 2009, Kim et al. 2016, Park et al. 2016). Reduced shoot density with increasing water depth has been reported frequently in seagrasses, which is a meadow-scale response to reduced light availability (Olesen et al. 2002, Collier et al. 2007, Kim et al. 2016, Park et al. 2016, Sugimoto et al. 2017). In the present study, the shoot density of *Z. japonica* in the manipulated submerged conditions decreased to less than half of that in the intertidal conditions by the end of the experiment. A reduction in *Z. japonica* density with increasing water depth was also observed in Hiroshima Bay, Japan (Sugimoto et al. 2017). Competitive interaction for irradiance among subtidal seagrasses, such as shading by the taller *Z. marina*, has been suggested to cause a reduction in *Z. japonica* shoot density in the lower intertidal zone (Kim et al. 2016). In the present study, *Z. japonica* shoots in the manipulated submerged conditions were much taller and may have been exposed to reduced light availability as a result of self-shading. Thus, reduction in light intensity caused by self-shading by taller shoots may have reduced *Z. japonica* shoot density in the submerged conditions of our study.
Seagrasses inhabiting intertidal areas can undergo photosynthesis during the emersion periods, suggesting that intertidal seagrasses can assimilate atmospheric CO$_2$ for photosynthesis when exposed to the air during low tide (Silva et al. 2005, Park et al. 2016). However, the atmospheric CO$_2$ assimilation by seagrasses, such as *Z. marina* and *Z. noltii*, significantly decreases when the water content of the leaf tissues decreases due to long leaf exposure to air (Leuschner et al. 1998, Kim et al. 2016). In the present study, *Z. japonica* in the intertidal conditions was regularly exposed to air for approximately 1–4 hrs daily, whereas the plants in the manipulated submerged conditions were consistently submerged even during low tide. *Zostera japonica* in the intertidal conditions could undergo inorganic carbon limitation under longer emersion conditions, even though this intertidal species exhibited a complex interaction of morphology and growth strategies at the whole-plant level to reduce desiccation stress (Shafer et al. 2007). Thus, *Z. japonica* in the manipulated submerged conditions may have had more favorable conditions for photosynthesis without inorganic carbon limitation during low tide periods and consequently exhibited higher leaf productivity.

Because seagrasses inhabiting intertidal zones are regularly exposed to the air during low tide, they are subjected to extreme environmental conditions, such as high photo-inhibitory irradiance, extreme high and low temperatures, and desiccation stress (Abe et al. 2009, Massa et al. 2009, Shafer et al. 2014). A smaller shoot height and leaf width and higher shoot density may improve the desiccation tolerance of seagrasses in the intertidal zone (Kim et al. 2016, Park et al. 2016). *Cymodocea rotundata* Asch. & Schweinf. and *Thalassia hemprichii* (Ehrenb.) Asch. have been reported to be significantly smaller leaf length and sheath area in the intertidal than in subtidal zones (Tanaka and Nakaoka 2004). The leaf length of these seagrasses decreased when the plants were transplanted from the subtidal to the intertidal zone (Tanaka and Nakaoka 2004). Shorter canopy heights and narrower leaf widths of *Z. marina* and *Phyllospadix iwatensis* Makino have also been reported in the intertidal zone compared with the subtidal zone on the Pacific coast (Yabe et al. 1996, Boese et al. 2005, Park et al. 2016). The reduction in seagrass shoot size, such as leaf length and width, in the intertidal zone has been considered an adaptive response to desiccation stress for better survival under emersion conditions (Tanaka and Nakaoka 2004, Boese et al. 2005, Park et al. 2016). A higher shoot density has also been suggested as an adaptation of seagrasses to desiccation stress by preventing drying of leaf tissues (Yabe et al. 1996, Park et al. 2016). Thus, the smaller shoot height and higher shoot density of *Z. japonica* plants in the intertidal conditions of the study sites in the present study probably served to improve their desiccation tolerance during low tide.

Although the growth responses of *Z. japonica* were different between the manipulated submerged and control intertidal conditions, the differences in growth between the two conditions were small at the end of the experiment in November. Growth of *Z. japonica* exhibits distinct seasonal variations, being highest in summer and lowest in winter (Zhang et al. 2015, Kim et al. 2016). The leaf productivity of *Z. japonica* increased continuously with increasing temperature in spring and summer, which suggested that this species may be well adapted to high temperature conditions (Shafer et al. 2008, Kaldy et al. 2015, Kim et al. 2016). In the present study, the growth responses of *Z. japonica* to the manipulated submerged and control intertidal conditions were very different during the high-temperature growing season in September, but were only slightly different during the low temperatures of...
November, indicating interaction effects between the submergence treatments and sampling season. *Zostera japonica* growth may have been strongly suppressed by the low temperature in both the manipulated submerged and the control intertidal conditions, and thus the submergence manipulation probably had little effect on *Z. japonica* growth at the end of the experiment in November.

Seagrasses inhabiting intertidal zones are vulnerable to the environmental changes associated with climate change, such as increasing water temperature and sea level rise (Short and Neckles 1999). However, the effects of sea level rise on seagrass growth and distribution will vary spatially (Chust et al. 2010). According to a habitat suitability model, suitable areas for *Z. noltii* growth in the Oka estuary, Spain, have possibly increased as a result of sea level rise, inducing landward migration, but anthropogenic barriers, such as construction and hardened shorelines, can impede the shifting of seagrass habitats landward (Valle et al. 2014). A 17% decline in seagrass coverage was predicted under a scenario with a sea level rise of 1.1 m in Moreton Bay, Australia, due to development in the coastal zone (Saunders et al. 2013). According to the results of our study, the submergence conditions will have both adverse and positive effects on *Z. japonica* growth and distribution. Morphological plasticity, such as longer leaves at the individual level and reduced shoot density at the population level, was an acclimatory response of *Z. japonica* to the submergence conditions. Biomass and leaf productivity were also increased in the submerged conditions because of the larger shoot size in this condition. Thus, the growth and distribution of the intertidal seagrass *Z. japonica* did not appear to be suppressed by the submergence conditions, which mimicked a rise in sea level due to climate change. Because the growth of *Z. japonica* was not suppressed by manipulation of the submerged conditions, the restricted distribution of this seagrass species in the intertidal zone cannot be explained entirely by inundation stress in the subtidal zone.

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