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Asymmetric root distributions reveal press–pulse responses in retreating coastal forests

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Abstract. The impacts of climate change on ecosystems are manifested in how organisms respond to episodic and continuous stressors. The conversion of coastal forests to salt marshes represents a prominent example of ecosystem state change, driven by the continuous stress of sea-level rise (press), and episodic storms (pulse). Here, we measured the rooting dimension and fall direction of 143 windthrown eastern red cedar (*Juniperus virginiana*) trees in a rapidly retreating coastal forest in Chesapeake Bay (USA). We found that tree roots were distributed asymmetrically away from the leading edge of soil salinization and towards freshwater sources. The length, number, and circumference of roots were consistently higher in the upslope direction than downslope direction, suggesting an active morphological adaptation to sea-level rise and salinity stress. Windthrown trees consistently fell in the upslope direction regardless of aspect and prevailing wind direction, suggesting that asymmetric rooting destabilized standing trees, and reduced their ability to withstand high winds. Together, these observations help explain curious observations of coastal forest resilience, and highlight an interesting nonadditive response to climate change, where adaptation to press stressors increases vulnerability to pulse stressors.

Key words: coastal storms; disturbance; ecosystem response; Juniperus viriginiana*; salinization; sea-level rise.*

Introduction

Understanding the mechanisms that lead to ecosystem state change is increasingly critical as the effects of climate change challenge the stability and resilience of ecosystems around the world (Walther et al. 2002, Doney et al. 2012, Kroël-Dulay et al. 2015). Climate change jeopardizes ecosystem stability on decadal to century time scales by exerting both long-term disturbances (presses) that gradually alter environmental conditions (i.e., sea-level rise, increasing temperature and CO_2 concentrations, ocean acidification), and sharply delineated, stochastic disturbances (pulses) that suddenly perturb an environmental setting (i.e., extreme climatic events) and exacerbate impacts of presses (Bender et al. 1984, Lake 2000, Harris et al. 2018, Jentsch and White 2019).

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Though ecosystems may adapt to a climate-driven press over time or recover from a pulse event, they are generally less resilient to the simultaneous impacts of press and pulse disturbances (Harris et al. 2018). Among the most prominent examples is the conversion of upland and freshwater coastal forests along the Atlantic and Gulf coasts of the United States to salt marsh (Williams et al. 1999, Langston et al. 2017, Fagherazzi et al. 2019, Kirwan and Gedan 2019, Schieder and Kirwan 2019). Relict forest stands develop as the press stress of increased salinity from sea-level rise exceeds the tolerance threshold of tree seedlings. Droughts and coastal storms punctuate the stress of sea-level rise, causing high rates of mortality among mature trees (Williams et al. 2003, DeSantis et al. 2007, Fernandes et al. 2018). Gradually, forest stands transition to salt-tolerant shrubs, which are eventually replaced by salt marsh (Langston et al. 2017). Though previous work has evaluated the separate roles of gradual sea-level rise and pulse events on forest loss, the combined effects of these press and pulse disturbances on coastal forest loss remain unclear and spatially heterogeneous.

Here we aim to understand the interactive role of press (sea-level rise) and pulse (episodic storms) disturbance by examining tree roots exposed during large wind events in a rapidly retreating Chesapeake Bay coastal forest. We find that eastern red cedar (*Juniperus virginiana*), one of the most salt-tolerant coastal tree species, disproportionately distributes its roots upslope, towards potential sources of freshwater. This asymmetry results in resistance to saltwater intrusion, but may lead to greater susceptibility to windthrow during pulse storm events.

Methods

We measured the fall direction and root characteristics of windthrown trees along the York River, a tributary of the Chesapeake Bay (Virginia, USA). This region is part of the mid-Atlantic sea-level rise hotspot, with relative sea-level rise rates 2–3 times the global average due to a weakening Gulf Stream and rapid land subsidence (Erdle and Heffernan 2005, Sallenger et al. 2012). The gently sloping coastal plain and high rates of relative sea-level rise have led to the rapid transition of forests and agricultural fields to marsh. Since the late 19th century, more than 400 km^2 of Chesapeake Bay uplands have been replaced by marshes (Schieder et al. 2018), with a rate that has accelerated in parallel with relative sea-level rise (Schieder and Kirwan 2019).

Our study site, the Catlett Islands, are a series of east–west forested ridges consisting primarily of loblolly pine (*Pinus taeda*) at higher elevations and red cedar at the marsh-forest boundary (37°18′ N; 76°33′ W, Fig. 1a). Nearby coastal forests are retreating at rates up to 5 m/yr, and have accelerated in parallel with 20th-century sea-level rise (Schieder and Kirwan 2019). Although most retreating coastal forests are characterized by standing dead trees (i.e., ghost forests), our site was uniquely characterized by numerous windthrown trees with exposed root plates. The abundance of uprooted trees allowed us to measure the characteristics of exposed roots in order to examine how trees may adapt to both pulse (large storm events) and press (salt water intrusion) stressors.

We measured the size and fall characteristics of 143 windthrown adult eastern red cedar (*Juniperus virginiana*) trees. Only individuals with a portion of their root plate still buried or with large quantities of soil still attached were measured to ensure the tree fell in place and was not disturbed. We assume that these trees are indeed windthrown, and not uprooted by subsidence, erosion, or the development of highly asymmetric canopies. This interpretation is consistent with previous observations of windthrown cedar trees near the marsh–forest boundary (Williams et al. 1999), exposure to marine winds, shallow rooting, and a location away from the influence of wave erosion.

Circumference at breast height, cardinal fall direction, and topographic aspect were measured for each individual windthrown tree. Aspect refers to the direction of steepest slope (i.e., the downslope, seaward, or marsh-facing direction). We compared fall directions to buoy wind data measured since 2016 at the mouth of the York River, away from obstructions from buildings and trees (NOAA, York Spit Buoy 44072). We extracted the wind speed and direction of winds >15 m/s from the full 15-min data set, which represent the strongest (~99th percentile) winds on record during the measurement period. Because sampling was done on all sides of elliptical islands, and in a relatively protected system, we assume that any bias associated with the orientation of the shoreline relative to predominant winds is minimal. We then measured the size and spatial distribution of the exposed root plates, including the length of the longest root in each direction, the number of first-order roots, and the circumference of the largest root in the downslope and upslope (180° from downslope) direction (Fig. 1b). Root length was measured as the straight-line distance from the central meristem in each direction (i.e., curves were ignored). In cases where any portion of the root was buried, length was measured only to the soil surface. The circumference of the largest first-order root was measured 10 cm from the central meristem. Rooting characteristics were missing for nine individuals, so all calculations of length, circumference, and number of roots have an $N = 134$. We did not observe any uprooted loblolly pine across the entire study site. Therefore, this study focuses entirely on the rooting characteristics of red cedar, the tree that most typically defines the seaward limit of coastal forests in the region (Brinson et al. 1995).

Results

Windthrown cedars fell in nearly every cardinal direction (0–360°) but a large number fell towards the southwest (~225°) and west (~280°; Fig. 2a). In contrast, high-speed wind events (>15 m/s) in the area originate primarily from the north (Fig. 2b). The direction of windthrow was strongly correlated with topographic aspect. Of the 143 trees measured, 123 fell within ±90° of the upslope direction and half (70) of all trees fell within 45° of the upslope direction (Fig. 2c).

The exposed root plates were highly asymmetric, with roots disproportionately distributed in the upslope direction, and away from saltwater sources in the downslope, seaward direction. Upslope roots were, on average, greater in length ($\overline{L}_U = 119 \pm 7.6$ cm; mean ± SE), circumference ($\overline{C}_U = 74 \pm 3.1$ cm), and number ($\overline{N}_U = 2.1 \pm .07$) than downslope roots ($\overline{L}_D = 77 \pm 4.1$ cm, $\overline{C}_D = 39 \pm 1.9$ cm, $\overline{N}_D = 1.6 \pm .05$). Additionally, the ratios of these metrics ($R_{L,C,N}$) for individual trees strongly favored the upslope roots (e.g., $R_L = L_U/L_D$ for each individual tree; Fig. 3a–c). We classified every tree with a full set of root measurements ($n = 134$) as either upslope dominant ($R_x > 1$) or downslope dominant ($R_x < 1$) for each metric. Out of 134

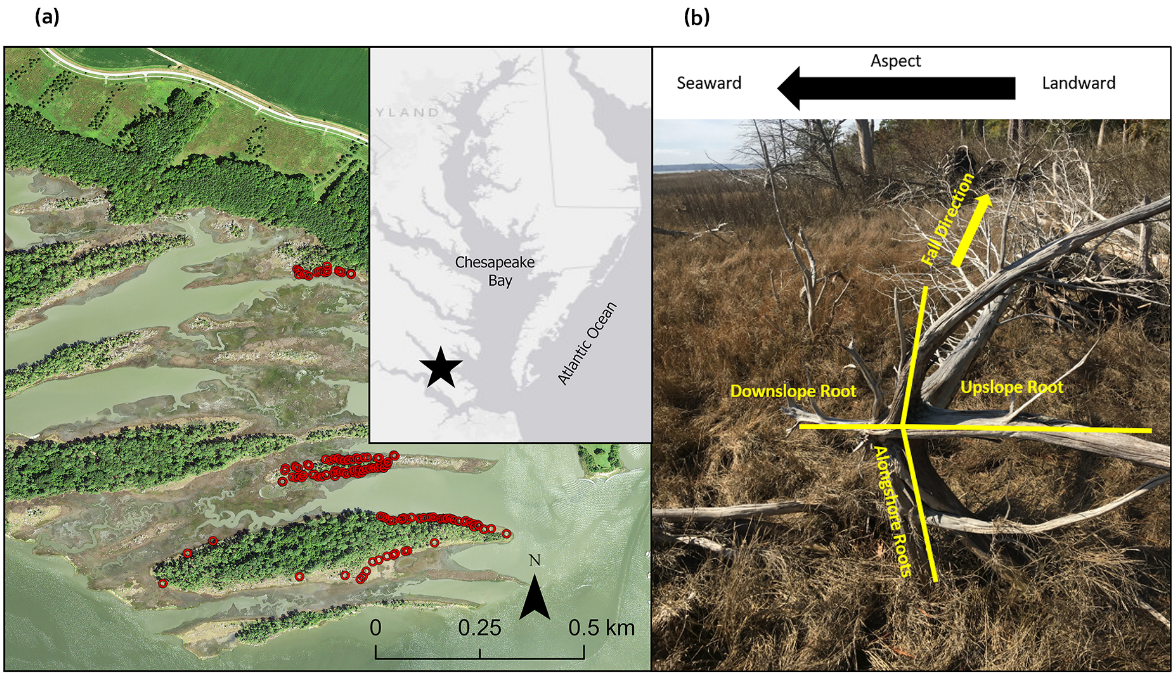

Fig. 1. (a) Aerial photograph of the Catlett Islands study site (Virginia, USA), where red circles denote measured windthrown trees in a rapidly retreating coastal forest. (b) The exposed root plate of a windthrown eastern red cedar, illustrating root asymmetry in our study area. The schematic illustrates the measured roots and fall direction relative to the aspect, where the uphill direction (forest) is towards the top right and the downhill direction (marsh) is toward the bottom left. Downslope roots were oriented towards the salt marsh, upslope roots were oriented towards the forest, and alongshore roots were oriented parallel to the marsh–forest boundary. In the photograph, the size and length of roots are dominant in the upslope direction.

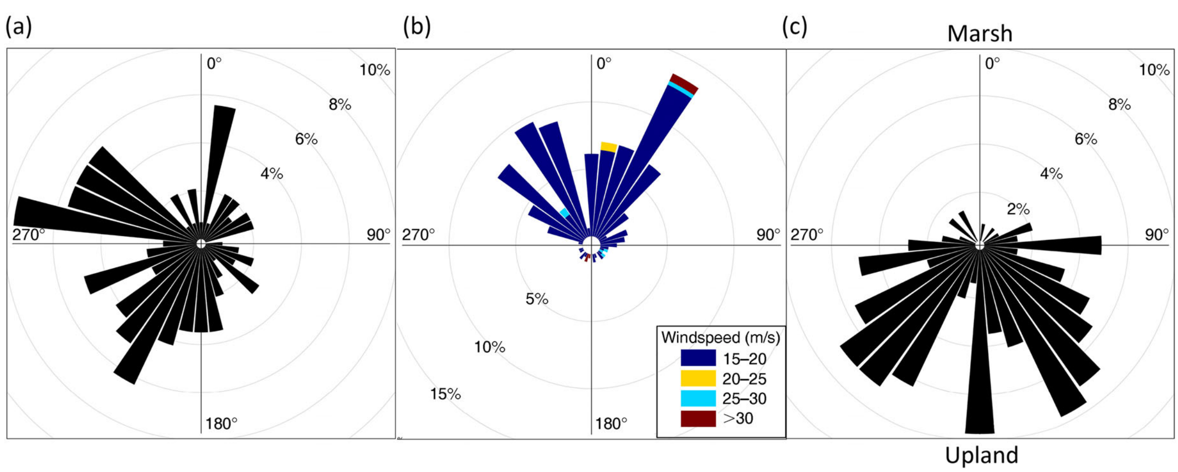

Fig. 2. Rose diagram of (a), (c) tree-fall direction and (b) wind direction in an eastern red cedar coastal forest. In (a), tree-fall directions are oriented in their cardinal direction, where the top of the rose diagram indicates a northward fall direction. In (b), wind directions are oriented in their cardinal direction (i.e., top = north), and represent the highest 1% of winds (>15 m/s) measured at the York Spit Buoy, Chesapeake Bay, Virginia. In (c), fall directions are oriented relative to topographic aspect, where the top of the rose diagram represents downslope direction.

trees, 111 were upslope dominant in circumference ($\overline{R}_C = 2.7$), 82 trees were upslope dominant in length (average ratio, $\overline{R}_L = 2.3$), and 70 trees were upslope dominant in number ($\overline{R}_N = 1.5$, where 56 trees had $R_N = 1$, and only 8 trees had $R_N < 1$). Differences between upslope and along-shore root directions were more subtle. The average alongshore root was equal in length to the upslope root (117 ± 4.6 cm). A majority of trees were alongshore dominant in length (n = 81), but the average ratio favored the upslope direction ($\overline{L_U/L_A}$ = 1.3). Nevertheless, because root lengths were measured to the ground surface, and many of the upslope roots were buried, upslope root lengths and their associated ratios are underestimates, resulting in a conservative measure of root asymmetry in the upslope direction.

Discussion

Conceptual and numerical models typically assume that sea-level rise leads to passive retreat of coastal ecosystems, where forests do not actively adapt to saltwater intrusion (Brinson et al. 1995, Doyle et al. 2010, Fagherazzi et al. 2019, Kirwan and Gedan 2019). For example, marsh migration models assume that migration can be predicted on the basis of sea-level rise and topography alone, and that marshes instantaneously replace forests when tidal inundation exceeds some threshold elevation (Enwright et al. 2016, Kirwan et al. 2016). In reality, increased soil salinity and tidal flooding associated with sea-level rise create heterogeneous spatial patterns of forest retreat and forest stand structure (Williams et al. 1998, 1999, DeSantis et al. 2007, Langston et al. 2017). Our work shows red cedar roots are most prominent in the upslope direction (i.e., away from the leading edge of soil salinization and towards freshwater sources; Fig. 3a, b). We propose that this root asymmetry represents an active physiological adaptation to chronic salt stress, but makes them more vulnerable to windthrow, and contributes to variable patterns of forest retreat.

Root-system structure is largely shaped by roots actively seeking resources required for plant growth and survival (Lynch 1995, Zanetti et al. 2014, Centenaro et al. 2018). For trees in coastal upland and freshwater forests, increased soil salinity from sea-level rise compromises access to fresh groundwater, a resource fundamental to their survival that shapes rates of forest retreat (Williams et al. 1999, Saha et al. 2011). Disproportionately longer, larger, and more frequent roots in the upslope direction compared to downslope roots (Fig. 3a–c) suggests a positive hydrotropic response by red cedar (i.e., elongated roots and growth directed towards high water potential) to reach necessary fresh groundwater (Jaffe et al. 1985, Krauss et al. 1999, Cassab et al. 2013, Dietrich 2018). Diminutive downslope roots are consistent with responses of modified root growth employed by plants to minimize damage from salt toxicity (Galvan-Ampudia and Testerink 2011, Rewald et al. 2012). Asymmetrical root systems,

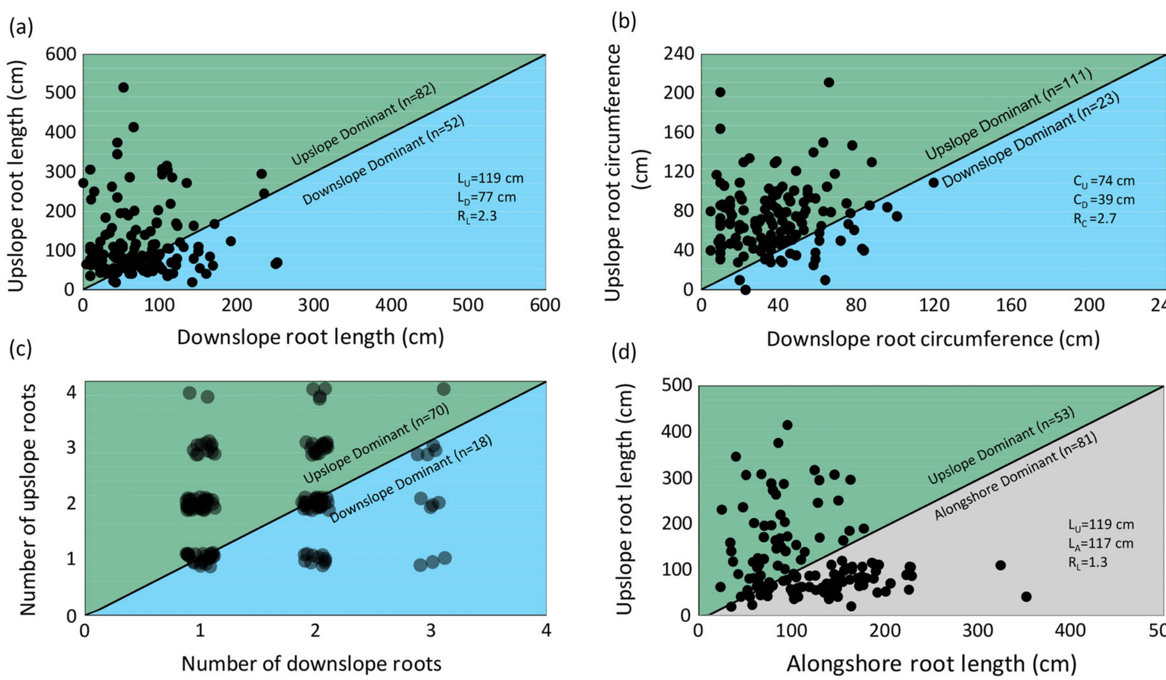

Fig. 3. Rooting characteristics of individual windthrown eastern red cedar trees in upslope (i.e., towards freshwater) and downslope (i.e., towards salt marsh) directions. Panels (a)–(c) report (a) the length, (b) largest circumference, and (c) the total number of primary roots. (d) Average root length in the upslope and along-slope directions. Data points represent individual trees, where points above the 1:1 line represent trees with rooting characteristics that are dominant in the upslope direction. Also shown are the average length ($\overline{L}_U$, $\overline{L}_D$) and circumference ($\overline{C}_U$, $\overline{C}_D$) of all trees in the upslope and downslope directions, and the average ratio between them for each individual tree ($\overline{R}_L$, $\overline{R}_C$).

including the development of prominent upslope roots, have also been observed in many other tree species seeking fresh groundwater (Tsutsumi et al. 2004, Zanetti et al. 2014). Hence, physiological and morphological plasticity of roots across species to environmental conditions supports our interpretation that asymmetrical root structure in red cedar is an active physiological adaptation rather than simply an intolerance to saline soils.

Our finding that adult red cedars have disproportionally larger root networks in the landward direction in a submerging coastal forest helps explain curious patterns of forest resilience (Kirwan et al. 2007, Field et al. 2016). For example, rates of radial growth and mortality were no higher near the marsh edge than in the forest interior in a mixed-hardwood forest in coastal Connecticut, dominated by species known to be among the most intolerant to salt (Field et al. 2016), and the effects of sea-level rise on radial growth in other tree species are inconsistent (Robichaud and Begin 1997, Kirwan et al. 2007). Moreover, mortality of adult trees tends to lag behind changes in sea level and mortality of seedlings (Williams et al. 1999, Kirwan et al. 2007, Langston et al. 2017, Fagherazzi et al. 2019). Long roots in the uphill direction of adult trees could mitigate interannual fluctuations in soil conditions directly under the tree, and facilitate tree survival in locations that would otherwise be unconducive to tree survival. In forests adjacent to steeper uplands, even slightly longer roots would enable access to water from higher-elevation soils less impacted by salt. Thus, an asymmetric root network could also help explain why differences in forest retreat rates throughout the mid-Atlantic coast are not easily explained by spatial variability in relative sea-level rise rate and the slope of adjacent uplands (Schieder et al. 2018, Fagherazzi et al. 2019, Schieder and Kirwan 2019).

Our results also suggest that physiological adaptation to long-term salinization makes red cedar more vulnerable to episodic wind events. In the absence of salinity, red cedars develop a lateral, fibrous root system in shallow or saturated soils, with first-order roots reaching lengths of up to 6 m in all directions (Lawson 1990). However, we find that roots at the marsh–forest ecotone are highly asymmetric, with root lengths in the downslope (seaward) direction typically less than 1 m (Fig. 3 a). The idealized root structure for withstanding high winds is a symmetrical root plate with approximately 2–3 major windward roots, and a few large, deeper leeward roots (Coutts et al. 1999, Danjon et al. 2008, Fourcaud et al. 2008). Large windward roots have been shown to provide 25% of total anchorage strength in deep-rooted trees (Yang et al. 2017) and up to 75% of total anchorage strength in shallow-rooted trees (Crook and Ennos 1996). In contrast, we find that large roots are prevalent only in the upslope direction, regardless of shoreline orientation or predominate wind direction (Fig. 3a–c). We suggest that the lack of windward roots makes these trees prone to windthrow, as evidenced by tree-fall directions that are consistently in the upslope direction (Fig. 2b).

Under the conventional press–pulse framework, press–pulse disturbances are considered additive stresses that collectively perturb a system beyond its tolerance threshold (Bender et al. 1984, Lake 2000, Scheffer et al. 2001, Harris et al. 2018, Jentsch and White 2019). For example, in terrestrial forests, pulse outbreaks of insect and disease exacerbate background mortality rates of stands stressed by increased temperatures and reduced resource availability (Weed et al. 2013, Allen et al. 2015). Similarly, tree stress from decreased water flow intensified by droughts and heat waves leads to riverine forest decline (Harris et al. 2018). In our system, coastal forest retreat is traditionally explained by the additive effects of seedling mortality from sea-level rise and tree mortality from coastal storms (Williams et al. 1999, 2003, Langston et al. 2017, Kirwan and Gedan 2019, Ogurcak et al. 2019). Granting that additive stresses of press–pulse disturbances jeopardize ecosystem stability, this perspective only considers ecosystem responses based on its tolerance to external stress. Generally overlooked are interactive responses by the perturbed system that may further intensify impacts from press–pulse disturbances.

We posit that red cedar trees increase their resistance to sea-level rise via physiological root responses that allow them to seek fresh groundwater and avoid saltwater. These responses result in an asymmetrical root morphology that in turn destabilizes standing trees, making them more vulnerable to windthrow during storm events. Thus, our work suggests a unique interactive response to press–pulse stressors, where root adaptations to long-term sea-level rise increases tree mortality from episodic wind events. This scenario differs from conventional press–pulse theory in that *adaptation* to chronic stress (i.e., sea-level rise) is increasing the vulnerability to episodic stress (storms), rather than the *tolerance* to two additive stressors determining system vulnerability. Moreover, as the dominant forest species of the marsh–forest ecotone along large sections of the U.S. Atlantic Coast (Brinson et al. 1995, Williams et al. 1999), the interactive response of red cedar is not only a species response, but also defines an ecosystem-level response to press–pulse disturbances, where forest mortality results in a fundamental shift to a salt marsh ecosystem. Together, these findings help broaden conventional press–pulse theory to include nonadditive effects, provide a mechanistic explanation for curious patterns of coastal forest retreat, and suggest that simple topographic projections may miss important physiological adaptations that potentially govern the response of coastal forests to sea-level rise and storms.

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