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The World's Tallest Tropical Tree in Three Dimensions

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Here we report the recent discovery of the world's tallest tropical tree (*Shorea faguetiana)*, possibly the world's tallest angiosperm (flowering plant), located in the rainforests of Sabah, Malaysian Borneo. In addition, we provide a novel three-dimensional exploration of the dimensions of this remarkable tree and use these data to speculate on what drives the limits of tree height. Through consideration of both mechanical (risk of wind damage) and ecophysiological constraints we argue that this tree is close to the maximum height possible for angiosperms, around 100 m, and discuss more broadly what the nature and location of this tree imply about the limits to tree height. We propose to name this remarkable tree "Menara," Malay for "tower."

This tall tree ("Menara") was first identified during an airborne Light Detection and Ranging (LiDAR) survey conducted in 2014. The tree is located in the Danum Valley Conservation Area (DVCA) in Sabah, which also holds the previous record holder for tallest tropical tree[1]. This tree is located at an elevation of 436 m a.s.l on a slope of 33° and an aspect of 72°. Because airborne LiDAR is prone to significant errors when used to estimate heights of individual trees (Wan Mohd Jaafar et al., 2018), and because hilly topography will likely exacerbate those errors, record claims need to verified by reliable and calibrated instruments (such as Terrestrial Laser Scanning [TLS]) and, ideally, manual tape measurement. Hence, following the airborne identification, researchers returned in August 2018 to manually measure trunk diameter and conduct TLS scans and a drone flight to construct a detailed 3D model (**Figure 1**) and to calculate tree height and other dimensions[2]. A further visit was conducted in January 2019, during which the tree was climbed to the top of its crown so the height could be directly verified with a measuring tape (**Figure 2**).

[1]The tallest tropical tree that has been locally climbed and measured is a 94.1m *Shorea faguetiana* reported in the Danum Valley Conservation Area in 2017 (https://www.theborneopost.com/2017/03/11/worlds-tallest-tropical-tree-in-danum-valley/), the tallest of 50 tall trees reported from an airborne lidar survey in 2016 (https://news.mongabay.com/2016/06/tropics-tallest-tree-found-in-malaysia/). In May 2018 a media report suggested a taller tree has been measured in Tawau Hills National Park, in Sabah (http://www.dailyexpress.com.my/news.cfm?NewsID=125818).
[2]3D data are available for download at https://doi.org/10.5287/bodleian:KzNpxEOg5, 3D data are viewable at https://skfb.ly/6KXXH, and UAV footage is viewable at https://www.eci.ox.ac.uk/news/2019/0408.html.

FIGURE 1 | A 3D point cloud of the tallest tropical tree generated from fusing 2 data sources: TLS pointclouds from a RIEGL VZ-400 (RIEGL Laser Measurement Systems GmbH); and pointclouds derived from applying structure-from-motion algorithms to video from a UAV flight up and around the tree. Still images were extracted from the UAV-based video footage using ffmpeg, and these were then used to create pointclouds using Pix4Dmapper software package (Pix4D SA,. Switzerland). The TLS and UAV-dervied pointclouds were fused together using CloudCompare software (version 2.10.1, retrieved from http://www.cloudcompare.org/), and the TLS points were colored based on the color of the nearest neighboring UAV point. Interactive data and downloads can be found at https://skfb.ly/6KXXH and Shenkin et al. (2019).

"Menara" is a *Shorea faguetiana* tree (common name Yellow Meranti), of the Dipterocarpaceae family, a taxon that dominates the humid lowland rainforests of SE Asia. As verified by measuring tape, it has a height of 100.8 m (distance to lowest part of the buttress; distance to lowest part of bole is 98.90 m, distance to highest base point of bole 96.26 m). This tree exceeds previous record holders including another tree in Danum Valley estimated at 94.1m by airborne LiDAR (ALS) in 2016 as well as a media report of a 96.9m *Shorea faguetiana* recorded in Tawau Hills National Park, Sabah, in May 2018[1]. This makes it

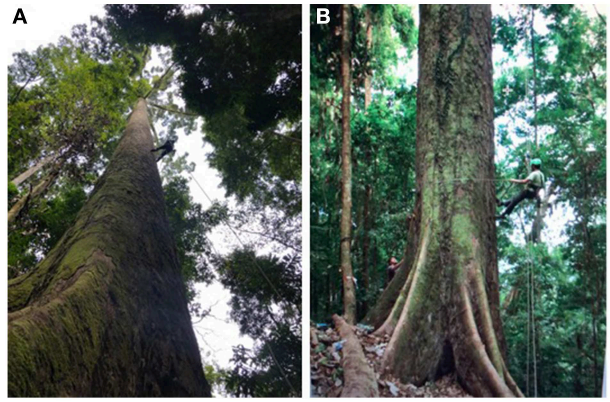

FIGURE 2 | Jamiluddin (Unding) bin Jami climbing the tree in January 2019 to verify its **(A)** height and **(B)** diameter above buttress.

unambiguously the tallest tropical tree yet recorded anywhere in the world.

The tree is also potentially the tallest angiosperm (flowering plant). From the lowest point of the buttress, "Menara" exceeds the 99.67 m record of tape-drop measurements of the "Centurion" tree in 2016, a *Eucalyptus regnans* in Tasmania, Australia[3]. Debates in protocols in how height-to-base is defined (to the lowest above-ground point, or to the median or mean ground-level point), and uncertainty in more recent rangefinder measurements of "Centurion" (Larjavaara and Muller-Landau, 2013) leave some room for ambiguity between these two giant trees, but "Menara" is now clearly a contender for the world's tallest angiosperm. For comparison, the tallest gymnosperm on record is the "Hyperion", a coastal redwood (*Sequoia sempervirens*) in California with a height of 115.7 m (Sillett et al., 2010)[4].

The TLS scan and drone flight enable us to establish additional dimensional information about this tree, and thus examine the mechanics of such giant trees. Using literature values of wood density for this species, we estimate that the tree has an above-ground fresh biomass of 81,500 kg (dry biomass 77,400 kg), of which only 5% is in the crown (which has diameter 40 m) and 95% is in the trunk. The stem is very straight, with the center of mass at 28 m above the ground and only displaced by 0.6 m from the central vertical axis, suggesting this tree is highly symmetrical and well-balanced despite being situated on strongly sloping ground. Menara's diameter above the buttress is 212 cm (**Figure 2B**). This conforms with the general and remarkably slender architecture of dipterocarp trees; in stark contrast, the Centurion eucalyptus has a diameter of 405 cm.

Tree height may be limited by mechanical, ecophysiological, and hydraulic constraints (Niklas, 2007), and perhaps also by

[3]Recent (2018) measurements by rangefinder suggest that the Centurion tree may have attained 100.5 m, but laser rangefinder measurements carry greater uncertainty and this value has not yet been verified by tape-drop. https://www.thetreeprojects.com/news/australias-tallest-tree-surpasses-metres.

[4]https://www.sfgate.com/bayarea/article/HUMBOLDT-COUNTY-World-s-tallest-tree-a-2550557.php.

genetic programming (Becker et al., 2000). Is this tree near the likely mechanical limits for angiosperm tree height? By having a spreading crown and therefore a high center of mass, most simple-crowned angiosperms are likely to have stronger mechanical constraints on their height than gymnosperms with a more tapering architecture (Jaouen et al., 2007). Interestingly, the tall *Eucalyptus regnans* appears to have a very different, superficially somewhat gymnosperm-like architecture, with a wide trunk diameter and short branches extending throughout much of its length. An analysis based on the three dimensional model of Menara (Jackson et al., 2019b) suggests that this tree is a long way from buckling under its own weight (it would need to attain approximately 255 m in height to hit that threshold), but is vulnerable to breakage under moderate wind speeds, and therefore may be close to a wind-related maximum height constraint. The methods employed in this mechanical analysis are excluded here for readability, but are explained in detail in (Jackson et al., 2019a).

The tree is partially sheltered by a ridge and is in a local topographic low-point, which is likely to have facilitated its growth to record heights. The effect of this ridge as a form of shelter from wind is clear from the differences in average tree heights on either side of the ridge (**Figure 3A**). Spatial patterns of tree heights across the DVCA in relation to aspect (**Figure 3C**) and slope (**Figure 3D**) suggest that the tallest trees (>70 m) may only reach such heights on aspects sheltered from the prevailing wind and with a slope steep enough to act as a wind barrier. This distinct spatial patterning of the largest trees in relation to topography suggests that wind stress may be the prevailing constraint on maximum tree height.

Ecophysiological constraints may also play a role. Jensen and Zwieniecki (2013) examined the basic physiological and geometrical constraints of the carbohydrate distribution network (pumping sugars from the leaves to the rest of the tree) and argued that, under ideal conditions (good moisture supply and low wind speed, as found in Sabah), the maximum possible height of angiosperm trees should be 104 ± 6 m. They show from an examination of leaf size data (predominantly from tropical SE Asia) that leaf size becomes increasingly constrained with increasing height, and that above $\sim$100 m height angiosperm leaves cannot maintain sufficient carbohydrate transport speeds in the phloem to maintain tree metabolism. Hydraulic constraints may also play a role: as trees grow taller, large negative pressures due to the weight of the long water columns suspended from crown to soil may ultimately limit leaf expansion and photosynthesis, even with ample soil moisture. From ecophysiological studies of California redwoods, Koch et al. (2004) predicted a maximum gymnosperm tree height of 122–130 m. Angiosperms, with their generally more efficient but less conservative hydraulic networks, are likely to be more constrained than gymnosperms by hydraulic constraints. These hydraulic constraints may drive limits to

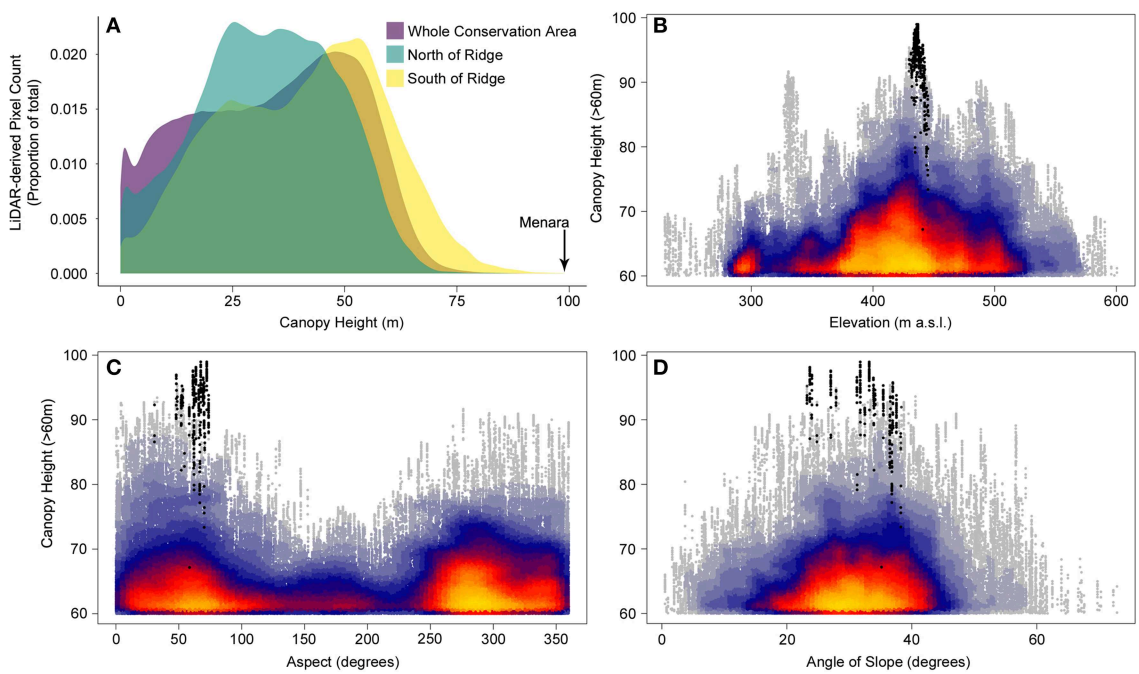

FIGURE 3 | (A) The count of LiDAR derived canopy heights for the local area surrounding the tree showing the difference in average tree heights on either side of the ridge in comparison to the DVCA as a whole. Relationship between canopy height for the tallest trees (>60 m) and **(B)** elevation, **(C)** aspect and **(D)** angle of slope. Black points represent pixels within the crown boundary of Menara. The airborne LiDAR data were collected by the UK Natural Environment Research Council (NERC) Airborne Research Facility (ARF) in 2014 using a Leica ALS50-II LiDAR system at an average point density of 2.9m-2. Data were first preprocessed on NERC's Data Analysis Node, with further processing carried out in LAStools. Topographic data for the DVCA polygon was extracted and analyzed with the R programming language (R Core Team, 2019), and topographic variables were calculated using the *raster* R package (Hijmans, 2019).

tree height (Liu et al., 2019), and the valley where this tree is located may ameliorate these hydraulic limits by maintaining humid soils.

Recent studies have shown that tall trees may be especially vulnerable to droughts (Bennett et al., 2015; Shenkin et al., 2018), likely because they are already close to hydraulic limits. Droughts in Borneo are associated with elevated tree mortality rates (Leighton and Wirawan, 1986; Woods, 1989; Nakagawa et al., 2000; Van Nieuwstadt and Sheil, 2005), and droughts across the tropics are expected to increase in depth and frequency as climate change proceeds (Malhi et al., 2008). In Borneo, annual precipitation has dropped by over 700 mm annually since the 1950s, likely due to land use change (McAlpine et al., 2018). Tall trees such as this *Shorea faguetiana*, which tend to have more cavitation-prone xylem (Liu et al., 2019), may therefore be vulnerable to these changing drought regimes. Perhaps due to its position near a valley bottom, "Menara" may be somewhat insured against droughts; indeed, its crown and foliage appear full and healthy. Thus, valleys may create multiple abiotic conditions that allow trees to grow taller than they would be able to otherwise.

Are there likely to be taller trees out there? The recent spate of records derived from airborne LiDAR surveys[1] suggests that taller tropical trees may yet be found: we predict that they are almost certainly in northern Borneo, will be of the genus *Shorea* and probably the species *Shorea faguetiana*, and they will be found in similarly sheltered locations in the local topography. Given the evidence of mechanical (wind) and ecophysiological constraints as outlined above, it is unlikely that any new tree would be much taller, but probably tall enough to unambiguously break the record for tallest angiosperm. Hence it is likely that the world's tallest extant flowering plant still sits undiscovered somewhere in the forests of Borneo.

This work highlights that in the world's tropical rainforests some of the largest organisms on Earth still await discovery and description. Over the past decade the Sabah Forestry Department has progressively extended the protection of several hundred thousand hectares of forest in the vicinity of the Danum Valley Conservation Area—which is now buffered on all sides by totally protected areas (Reynolds et al., 2011). Further, the Sabah Government has committed, by 2025, to increase the extent of protected forests to 30% of the State's land area (Sabah Forestry Department, 2018). The discovery of this remarkable tree provides additional recognition to, and impetus for, efforts to conserve these magnificent, biodiverse and record-breaking tall rainforests.

AUTHOR CONTRIBUTIONS

YM, AS, CC, and DSB wrote the manuscript with input from co-authors. The airborne lidar work and analysis was conducted by CC and DSB, and supported by GF, GR, MC, GvdH, DB, and DC. The terrestrial laser scanning was conducted by AS and supported by YM, MD, LB, and PW. The drone flights and point cloud analysis were conducted by AS. The tree was climbed and its tape height measured by JbJ. The tree mechanics analysis was conducted by TJ. The work in Malaysia was supported and facilitated by NM, RN, and GR.

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