Influence of wind and slope on buttress development in temperate tree species

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Abstract: A buttress is a prominent lateral-vertical structures of surface roots of a canopy or emergent trees frequently observed in tropical forests. Buttresses are probably formed to enhance mechanical stability of tree trunks and/or promote nutrient acquisition. However, the morphological diversity and control of buttress development remain unclear. Therefore, we aimed to clarify variations in buttress development related to prevailing wind and declination of tree trunks in warm temperate forests of Japan. We chose two pairs of forest sites with similar precipitation and geographical locations, but with contrasting wind regimes. Buttresses of two \textit{Castanopsis} species, \textit{C. sieboldii} and \textit{C. cuspidata}, were assessed, and the size and direction of the most developed buttress (MDB) were measured for each individual. The average MDB height at the stem of trees at the strong wind site, Sumoto, was less than half of that at the control site, Himeji. However, the result was the opposite at the other strong wind site, Muroto, and control site, Kochi. The average MDB length did not differ between the strong wind and control sites. MDBs were formed corresponding to the direction of the most frequent wind at strong wind sites but not at control sites. The direction of growth of MDBs was almost the same as that at slopes at all the sites. Our results suggest that wind loading likely influences the development of buttresses; however, its effect could also be site-dependent. These results suggest the potential roles of buttress formation on mechanical stability of trees, which have not been appreciated in temperate forests.

Keywords: buttress, \textit{Castanopsis cuspidata}, \textit{Castanopsis sieboldii}, root shape, slope, wind

Introduction

Trees consist of roots with different morphologies and functions; relatively thick and lignified coarse roots primarily provide support to the main trunk against external forces (e.g., gravity, wind, water, and snow loading) and storage of carbon, water, and nutrients. By contrast, relatively thin and physiologically active fine roots are involved in the uptake and transport of water, nutrients, and hormones, as well as to achieve symbiosis with mycorrhizal fungi (Hirano et al. 2020). In each root type, the functions mentioned above are tightly coupled to their morphologies, e.g., in coarse roots, given the same aboveground size, the development of tap root and horizontal roots strongly affects resistance to uprooting (Hirano et al. 2018). Root morphology also varies corresponding to many environmental variables, such as temperature, soil water depth, and nutrient availability (Jackson et al. 1996, Holdaway et al. 2011, Freschet et al. 2017, Hirano et al. 2018), indicating the adaptive roles of root morphology. Therefore, investigating the morphological diversity of roots and assessing the mechanisms of their diversity would provide insights into root functioning and species adaptation to the environment.

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A buttress is a prominent lateral-vertical structure of surface roots, typically associated with a canopy or emergent trees (Davis and Richards 1934, Abu Hanifa Mehedi et al. 2012). Its occurrence is centered in lowland tropical forests, and 23-51% of species are reported to form buttresses (ter Steege et al. 1997, Chapman et al. 1998, He et al. 2013). So far, two main explanations have been proposed for buttress formation: 1) it enhances mechanical stability of tree trunks (Henwood 1973), and 2) it promotes nutrient acquisition (Richter 1984). To enhance mechanical stability, buttresses act as tension roots to prevent inclination and uprooting of the main trunk against external forces, such as gravity and wind loading, by releasing tension from the tree base and dispersing it into large surface areas of the buttresses. Buttresses may also contribute to increased plasticity in tree architecture via alleviating asymmetry in crown loads. The second explanation was proposed on the basis of the observation that juvenile trees of some species show buttresses in the absence of a load brought about by asymmetry in the crown or due to wind loading. This hypothesis states that the formation of buttresses at the juvenile stage is a consequence of lateral extension of roots that enhances nutrient uptake via an increase in root surface area (Smith 1972). Recent studies have also pointed out the roles of buttresses in nutrient uptake even at the adult stage – large buttresses prevent runoff of water and nutrients from the upslope side, thus maintaining a relatively high availability of soil nitrogen (Pandey et al. 2011, Tang et al. 2011).

The formation and development of buttresses vary along climatic, edaphic, and topographic gradients. In tropical forests, the frequency of buttresses decreases as the mean annual temperature decreases (Smith 1972); it also increases in sheltered creeks than in exposed ridges and plateaus (Davis and Richards 1934). These authors also found that more developed buttresses are frequently observed in shallow soils where roots cannot penetrate deeply into soil layers. Regarding orientation of the buttresses, it has been reported that buttresses are frequently formed in the windward direction or on the opposite side of a trunk lean in tropical forests (Navez 1930, Richter 1984, Warren et al. 1988, Mattheck and Bethge 1990, ter Steege et al. 1997), which is consistent with the mechanical support hypothesis. Warren et al. (1988) suggested that although the direction of prevailing wind and that of trunk declination often cause buttress formation in a correlated manner, the latter influences buttress formation to a greater extent due to its constant and unidirectional nature; this view was also supported by Young and Perkocha (1994). On the contrary, several studies did not find any association between trunk declination and buttress formation (Davis and Richards 1934, Lewis 1988, Ruslandi et al. 2015), thus the mechanisms that control the development of buttresses still remain unclear.

In the present study, using two dominant woody species of trees in warm temperate forests of Japan, we aimed to clarify the variations in buttress development (size and direction) in relation to prevailing winds and declination of tree trunks. We chose two pairs of forest sites with similar precipitation and similar geographical locations, but with contrasting wind regimes (related to the frequency of strong winds and their prevailing directions). Based on the assumption that buttresses confer mechanical stability to tree trunks, we predicted that 1) trees growing at strong wind sites (with high frequency of strong winds) have large buttresses, and 2) buttresses are mostly formed on windwards sides for strong wind sites and on the opposite side of trunk leans for control sites. We studied the largest buttresses of trees because small ones might have functions other than mechanical support (Young and Perkocha 1994). To the best of our knowledge, this study is the first quantitative report on buttress development in temperate tree species.

Materials and methods

Research sites

Field measurements were conducted at four sites (two sites in Hyogo Prefecture: Sumoto (SMT) and Himeji (HMJ), and two sites in Kochi Prefecture: Muroto (MRT) and Kochi (KOC)) in western Japan (Figure 1-A, Table 1). To select the research sites, we referred to the strong wind indices defined by Yoneda (2020). strong wind indices are defined as relative cumulative frequencies of the maximum monthly instantaneous wind speed occurrence multiplied by 12 months. The values at the maximum wind speeds that are more than 24.5 m s⁻¹ and 32.7 m s⁻¹ are defined as Storm Index (SI) and Hurricane Index (HI), respectively. From a combination of SI and HI, SMT and MRT were selected as the points where both SI and HI were high throughout the year. HMJ was selected as corresponding to SMT, and KOC was selected as corresponding to MRT, where the climate and topography were similar but both SI and HI were low (Table 1).

The candidates for specific research sites for each area were decided by referring to the literature and maps (Yamanaka 1955, 1970; Higuchi 2006; Kochi Prefecture 2019). We targeted the genus...
Castanopsis, since Yamanaka (1955) have been reported that the genus Castanopsis form buttresses in several places. We also surveyed the woodlands in each area, in which the genus Castanopsis may have been distributed using an aerial photograph mode provided by Google map. We selected sites that comprised a natural forest dominated by evergreen broad-leaved trees. Finally, the research sites were chosen as described. The SMT research site was located at the Mikumayama Park in the southeastern part of the Sumoto City, which is located on the Awaji Island (Figure 1-A, Ba; N 34°20’, E 134°54’, 80±0 m a.s.l.). The HMJ research site was located on the west side of Mt. Masui (elevation 259 m) in the central part of Himeji City (Figure 1-A, Bb; N 34°52’, E 134°42’, 172±20 m a.s.l.). For the MRT research site, two areas were selected around Cape Muroto (Figure 1-A, Bc, and Bd). Furthermore, MRT 1 was located around the Hotsu-misaki Temple on the north side of Cape Muroto (N 33°14’, E 134°10’, 157±6 m a.s.l.), and MRT 2 was located around the Kasuga Shrine, about 35 km north of

| Site (Prefecture) | Site classification | Annual mean temperature (℃) | Annual mean precipitation (mm) | Annual mean wind speed (m s⁻¹) | Annual most frequent wind direction | Storm index | Hurricane index | Average slope ± SD (°) | Representative tree species |
|------------------|---------------------|-----------------------------|-------------------------------|-------------------------------|-----------------------------------|-------------|----------------|----------------------|-----------------------------|
| SMT (Hyogo)      | Strong wind         | 15.8                        | 1914                          | 2.5                           | North                             | 4.50        | 0.72           | 9.9 ± 7.1             | Castanopsis sieboldii       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Elaeocarpus sylvestris      |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Litsea coreana              |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Camellia japonica           |
| HMJ (Hyogo)      | Control             | 15.7                        | 1494                          | 2.6                           | Northwest                         | 1.12        | 0.18           | 9.3 ± 0.6             | Castanopsis sieboldii       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Castanopsis cuspidata       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Quercus serrata             |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Ilex pedunculosa            |
| MRT (Kochi)      | Strong wind         | 16.9                        | 2794                          | 6.8                           | East-northeast                     | 11.04       | 5.26           | 17.5 ± 8.6             | Castanopsis sieboldii       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Castanopsis cuspidata       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Cinnamomum camphora         |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Machilus thunbergii         |
| KOC (Kochi)      | Control             | 17.4                        | 2937                          | 1.7                           | West                              | 0.82        | 0.14           | 18.7 ± 5.4             | Castanopsis sieboldii       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Castanopsis cuspidata       |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Quercus glauca              |
|                  |                     |                             |                               |                               |                                   |             |                |                      | Cinnamomum camphora         |

Storm index (1/12 months) and Hurricane index (1/12 months) are defined by Yoneda (2020).

Fig. 1. Location of each research site (A), and locations of the examined buttresses at each research site (Ba-e); Sumoto (SMT), Himeji (HMJ), Muroto (MRT) and, Kochi (KOC). The map of the research sites was described by Quantum Geographic Information System (QGIS version 3.10.11-A Coruña).
Cape Muroto (N 33°31’, E 134°14’, 38±10 m a.s.l.). The KOC research site was located at Hitsuzan Park and Kochi Castle in Kochi City (Figure 1-A, Be; N 33°33’, E 133°31‘-32’, 55±37 m a.s.l.). The representative tree species found at each research site are summarised in Table 1.

The field measurement period was at the end of August 2020 at the SMT, MRT, and KOC sites, and mid-October 2020 at the HMJ site.

Fig. 2. Buttresses observed in *Castanopsis* species in (a) SMT, (b) HMJ, and (c) MRT.
Meteorological data

The observation values of annual average temperature, precipitation, and wind speed at each research site for the past 10 years up to 2019 were calculated from data obtained from the Japan Meteorological Agency database (Table 1). The maximum wind direction of the past 10 years up to 2019 was extracted from the “most frequent wind direction 16 directions (per month)” data provided by the Japan Meteorological Agency database (Table 1).

Measurement of buttress and acquisition of geographical information

Two Castanopsis species (Castanopsis sieboldii and Castanopsis cuspidata) with well-developed buttresses, fully matured, were searched visually at each research site. The root of both tree species is deep and many-branch type (Karizumi 2010). Lateral roots and the base of tree stem on shallow topsoil sometimes develop buttresses. A buttress is defined as “an enlarged and thickened root, in which the base of the horizontal root develops upward and is flattened in the vertical direction” (Dannoura 2020). In this study, horizontal roots that were exposed upwards from the ground surface and had a flat shape were defined as a buttress. The most developed buttress (MDB) in each individual tree was chosen for measurement.

For MDB, the horizontal length (from the trunk to the end of the buttress) and vertical height (from the tree trunk where the buttress emerged at the contact point with the ground surface) were measured. To characterise the shape of the buttress at each site, we created Height/Length index (H/L, height of the buttress root / length of the buttress root).

Information related to the direction and position of the trees was recorded using a GPS device (GARMIN eTrex Vista HCx, Garmin Ltd.). The slope of the place at which each tree was located was calculated from the intervals of the contour lines obtained from a topographic map (Geospatial Information Authority of Japan). The average slope was calculated by taking into account the number of trees measured at each research site. In this study, based on the observation that trees lean towards a downward slope (i.e., trees grow perpendicular to a slope), we assumed that the direction of slope and that of tree lean were the same. We also recorded the direction of the slope.

Statistical analysis

The Shapiro-Wilk test showed normality with H/L index, non-normality with the height and length of buttresses at each site. Therefore, we conducted the Kruskal-Wallis test on the height and length of buttresses, and ANOVA on the H/L index. Here, the height and length of a buttress and H/L index were specified as an objective variable, and the research site was specified as an explanatory variable. The significance level was corrected using the Bonferroni’s method. These statistical analyses were performed using R (The R Foundation for Statistical Computing, R version x64 3.6.1).

Results

Differences in buttress shapes between strong wind sites and control sites

We found five and seven trees with buttress roots at strong wind sites, SMT and MRT, and six trees at one of the control sites, HMJ (Fig. 2). The roots of trees located at KOC rose from the ground surface, but they did not exhibit a plate-like shape. Therefore, we defined these roots as buttress-like roots. The height of target trees was 6 – 12 m in SMT, 12 – 20 m in MRT, 13 – 15 m in HMJ, 8 – 16 m in KOC, respectively. The diameter at breast height of target trees was 26 – 40 cm in SMT, 30 – 70 cm in MRT, 52 – 166 cm in KOC, 35 – 82 cm in HMJ, respectively. The average MDB height at the stem of trees located at the strong wind site, SMT, was half of that at the control site, HMJ (Fig. 3a, \(P < 0.05\)). Conversely, the average MDB height at the stem of trees located at the other strong wind area, MRT, was more than twice that at the other control site, KOC (Fig. 3a, \(P < 0.05\)). Furthermore, we did not find a significant difference in the MDB length measured from the stem to the root tip in either pairs (Fig. 3b).

The H/L index in SMT (strong wind site) and HMJ (control site) was 0.34 ± 0.12 and 0.73 ± 0.11, respectively, showing no significant difference in buttress shape (\(P = 0.08\)). Also, the H/L index (0.60 ± 0.27) in MRT was similar to that in HMJ (\(P = 0.50\)). This indicates that the buttress shape in MRT, another strong wind area, was similar to that in the control area, HMJ. Our results also showed that the length and height at the stem were the largest in MRT among all the sites (Fig. 3). These results indicated that the shape of the buttress root was determined not only by the wind conditions, but also by other factors.

Relationship of the direction of buttress with that of wind and slope

At the strong wind sites, MDBs were formed in the similar direction as that of the most frequent winds in four out of five (SMT, Fig. 4a) and five out of seven trees (MRT, Fig. 4b). By contrast, at the
Fig. 3. Box plots of (a) the maximum height and (b) length from the trunk to the end of the buttress for the most developed buttresses (SMT, HMJ, MRT) and surface roots (KOC) at each site. Asterisks indicate statistically significant differences ($P < 0.05$) between two research sites.
control sites, the direction of the growth of MDBs was not necessarily the same as that at the most frequent wind direction (Fig. 4c, d). In HMJ, the directions of MDB formation were variable among trees; one tree developed MDBs in the downwind direction (Fig. 4c; B) and two trees showed MDB growth in the windward direction (Fig. 4c; A, F). In another control site (KOC), a tree exhibited the most developed buttress-like root in the downwind direction (Fig. 4d; C).

At the strong wind sites, four out of five (SMT) and six out of seven trees (MRT) formed MDBs on a downward slope (Fig. 4a, b). Similarly, in control sites, MDBs were formed by trees located on a downward slope in the case of four out of six trees (HMJ) and by all the trees located on slopes (KOC) (Fig. 4c, d). Thus, at all the sites, the direction of growth of the MDBs was found to be almost similar to that of the slope.

**Discussion**

Differently from prediction 1) that trees growing at strong wind sites have large buttresses, trees at strong wind sites did not necessarily develop larger buttresses than those at control sites (Fig. 3). The

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**Fig. 4.** Directions of buttress elongation, slope, and most frequent wind direction in (a) SMT, (b) MRT, (c) HMJ, and (d) KOC. Black lines denote the elongation direction of the most developed buttress of each tree. Dashed lines depict the direction of slopes for each tree. The grey bars show the most frequent wind direction for the decade at each site. The dashed italic letters identify each tree and the slope on it. Note: “A” in HMJ, “D” and “E” in KOC were not located on a slope.
height of MDBs was significantly different in one pair: higher in MRT (strong wind site) than in KOC (control site); however, this trend was reversed in another pair (HMJ and SMT, Fig. 3a). This suggests that wind loading likely influences the development of buttresses, which is consistent with previous studies (Richter 1984, Warren et al. 1988, Young and Perkocha 1994); however, its effect could also be site-dependent. The possible factors for the divergence could be differences at smaller spatial scales, including those in topography and soil structure (Davis and Richards 1934). Given the smaller differences in the average wind speed and frequency of strong winds in the HMJ and SMT pair than those observed in the KOC and MRT pair, factors other than wind might have had a greater influence on buttress formation by trees located at HMJ and SMT sites. On the other hand, the lengths of MDBs were not significantly different in both the pairs (Fig. 3b), suggesting that trees prioritize height growth rather than lateral growth for buttresses at strong wind sites. These results suggest that an increase in buttress height, but not length, is effective in reducing the risk of delamination at the stem-root transition area of trees growing on wind-exposed sites (Mattheyck and Bethge 1990).

Our prediction 2) that buttresses are mostly formed on windwards sides for strong wind sites and on the opposite side of trunk leans for control sites was partially supported by the results of this study: the orientations of MDBs corresponded mostly to the windward direction at strong wind sites (MRT and SMT, particularly for the former, Fig. 4a, b). On the contrary, although there were large variations, the orientation of MDBs corresponded more often to that of tree declination, but not on its opposite side, at control sites (HMJ and KOC, Fig. 4c, d). The former result suggests that wind loading likely influences the development of buttress at strong wind sites, consistent with the mechanical support hypothesis, which states that buttresses alleviate tension loads formed by wind (Henwood 1973, Richter 1984, ter Steege et al. 1997). However, the latter result apparently contradicts the mechanical support hypothesis, suggesting that the orientation of buttresses is not necessarily determined by mechanical loadings at control sites, rather it is influenced by small-scale factors, as discussed above. Such a phenomenon of independence between directions of wind and buttress formation was also observed in the tropical forests of Puerto Rico (Lewis 1988). In addition, because our study could not distinguish the effects of wind and trunk declination on buttress orientation because these two factors are correlated, particularly at SMT, further research should be conducted using more trees and sites to clarify the relative importance of these factors.

In conclusion, we assessed the formation of buttresses in temperate tree species and found that the development of buttresses varies among different sites and trees, presumably depending on the direction and strength of the wind. Our results suggest the potential role of buttress formation on mechanical stability in trees, which has not been appreciated in temperate forests. Japan is a relatively strong wind and moist region, with the occurrence of frequent typhoons in summer; thus, buttresses could play a role in lending mechanical support to trees, particularly for tall and wind-exposed tree species. Besides, there are many abiotic and biotic factors which might influence the formation and development of buttresses, such as depth and texture of soil and tree size (Richter 1984, Chapman et al. 1998, Woodcock et al. 2000, Newbery et al. 2009, Abu Hanifa Mehedi et al. 2012, He et al. 2013), which were not investigated in the present study. Therefore, considering the above factors, further studies should be carried out to clarify the key controls of buttress formation in temperate trees.

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