



Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador

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Abstract

Root architecture of tree species was investigated at two different altitudes in tropical forests in Ecuador. Increasing altitude was accompanied by higher wind speeds and more shallow soils, while slope angles of both sites were comparable (20–50°). Three tree species typical for the montane forest at 1900 m (*Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae), *Vismia tomentosa* Ruiz & Pav. (Clusiaceae)) and for the elfin forest at 3000 m (*Weinmannia loxensis* Harling (Cunoniaceae), *Clusia spec.* (Clusiaceae) *Styrax foveolaria* Perkins (Styraceae)) were examined. At 1900 m, 92% of the trees grew upright, in comparison to 52% at 3000 m. At 3000 m, 48% of the trees were inclined, lying or even partly uprooted. At this altitude, all trees with tap roots or with shoots connected by coarse rhizomes, 83% of the trees with stilt roots, and 50% of the trees in which stems or roots were supported by other trees grew upright, suggesting that these characteristics were relevant for tree stability. Root system morphology differed markedly between altitudes. In contrast to 1900 m, where 20% of structural roots originated in the deeper mineral soil, root origin at 3000 m was restricted to the forest floor. The mean ratio of root cross sectional area to tree height decreased significantly from $6.1 \times 10^{-3} \text{ m}^2 \text{ m}^{-1}$ at 1900 m to $3.2 \times 10^{-3} \text{ m}^2 \text{ m}^{-1}$ at 3000 m. The extent of root asymmetry increased significantly from 0.29 at 1900 m to 0.62 at 3000 m. This was accompanied by a significantly lower number of dominant roots at 3000 m (2.3 compared to 3.8 at 1900 m). In conclusion, native tree species growing in tropical montane and elfin forests show a variety of root traits that improve tree stability. Root system asymmetry is less important for tree stability where anchorage is provided by a deep and solid root–soil plate. When deep rooting is impeded, root traits improving the horizontal extension of the root–soil plate are more pronounced or occur more frequently. Furthermore, mutual mechanical support of roots and stems of neighboring trees seems to be an appropriate mechanism to provide anchorage in soils with low bulk density and in environments with high wind speeds.

Abbreviations: AR – aspect ratio; CSA – cross sectional area; DBH – diameter at breast height; ZRT – zone of rapid taper

Introduction

Tropical montane forests are often characterized by steep slopes and soil creeping (Hagedorn,

2001) and anchorage of trees is rendered difficult by shallow soils (Arraiga, 2000; Schrumpf et al., 2001). High wind speeds can cause additional mechanical loads. Hurricanes occur frequently in lower montane forests of Puerto Rico (Weaver, 2002) and were the main cause for tree mortality in a Mexican cloud forest (Arraiga, 2000). The

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combination of high mechanical stress and shallow soils typically leads to a short and stunted appearance of trees in such forests (Cavalier and Mejia, 1990; Cordero, 1999). Thus, trees require strategies to improve stability.

In mountain regions, trees are usually affected by wind loadings and “self loadings”. “Self loading” was defined by Chiatante et al. (2003a) as the mechanical stimulus due to the weight of a plant growing on a slope. To achieve anchorage, the tree transfers the loading forces experienced by the stem into the ground via roots (Chiatante et al., 2003a). Forces that trees and soil have to resist to maintain stability are mainly bending stress (within roots and stem), tension (within roots), compression (within and between roots and soil), and shearing forces (between root and soil and within soil) (Coutts, 1983; Crook et al., 1997; Czarnes et al., 1999; Nicoll and Ray, 1996; Nielsen, 1990; Stokes and Mattheck, 1996). Therefore, roots contribute to plant stability by forming rigid elements in the root system, e.g. deep taproots, or by forming a rigid root–soil plate.

Tree anchorage may also be related to various architectural root characteristics. Mechanical stress may cause an increase of total root cross sectional area (CSA) (Crook and Ennos, 1996; Mickovski and Ennos, 2003a, b). Another common response to mechanical stress is the modification of the shape of root cross sections (Chiatante et al., 2003a, b; Coutts et al., 1999). Often cross sections are T- or I-beam shaped (Nicoll and Ray, 1996; Rigg and Harrar, 1931) and eccentric (Mickovski and Ennos, 2003b). An extreme case of eccentric roots is buttresses (Crook et al., 1997). When the mechanical stress is not homogeneously distributed around the root system, root growth and development may be increased in the direction of maximal stress intensity influencing the symmetry of anchorage rigidity around the stem (Chiatante et al., 2003b; Coutts, 1983; Nicoll and Ray, 1996). Coutts et al. (1999) describe two types of root system asymmetry. Type I shows regular arrangement of individual roots around the stem center, but roots vary in diameter. In type II, roots are evenly sized but not uniformly arranged. In tree root systems both types of asymmetry may occur together. The direction of root clustering (windward/up-slope or leeward/down-slope) differs between studies (Chiatante et al., 2003b; Nicoll and

Ray, 1996; Watson, 2000). Root asymmetry is often assessed by the “center of mass” of all lateral roots. The “center of mass” is calculated by the sum of growth directions weighted by diameter or CSA of roots (Mickovski and Ennos, 2003b; Nicoll and Ray, 1996).

Most studies on root anchorage have concentrated on species of economical interest, particularly conifers (Crooks and Ennos, 1996; Cucchi and Bert, 2003; Mickovski and Ennos, 2003a, b; Moore, 2000; Nicoll and Ray, 1996; Polomski and Kuhn, 2001; Stokes, 1999; Watson, 2000). More knowledge about root morphology and architecture of other species is necessary to provide further insight into the way in which the form is related to the function of root systems (Mickovski and Ennos, 2003b). While the impact of strong winds in the elfin forest on the above-ground appearance of trees has been described by several authors (e.g. Cordero, 1999; Lawton, 1982), coarse root morphology of trees in this ecosystem has never been investigated. Very few studies deal with anchorage mechanisms of tropical plants and with anchorage mechanisms of plants growing on slopes (Chiatante et al., 2003a, b; Di Iorio et al., 2005). For tropical lowlands, architectural root traits of forest species are table roots and stilt roots (Crook et al., 1997; Jenik, 1978) as well as deep tap roots (Förster, 1970).

The aim of this study was to test the hypothesis that native species growing on steep slopes and exposed to high wind velocity are adapted to mechanical forces by the development of architectural root characteristics that improve anchorage in soil. Furthermore, it was expected that these root characteristics differ between altitudes because of differences in wind speed and in physical and chemical soil properties affecting root growth. To test this hypothesis, root architecture of three of the most frequent species growing in a tropical montane forest in the South of Ecuador at an altitude of 1900 m (montane forest) and 3000 m (elfin forest) was compared.

Material and methods

Study sites and species

Experimental work was carried out at the Estación Científica San Francisco (ECSF) near the

Podocarpus National Park in the South of Ecuador. The lower study site (1900 m a.s.l.; 03°58' S, 79°04' W) was located in a montane forest in the area of the ECSF. Thermally induced mountain breezes, i.e. valley winds during the day and mountain winds during the night, were typical for this region. Mean wind speeds measured at 2.5 m above soil surface in an open space outside of the forest were less than 2 m s⁻¹. Down-slope winds reached maximum speeds of 8 m s⁻¹ (M. Richter, pers. comm.). The soils had low pH_(CaCl2) in the range of 3–3.5, an average depth of the organic surface layer of 0.15 m and of the mineral soil of >0.9 m. Average bulk densities are listed in Table 1. Slope angles varied from 25° to 50°. At this altitude the tree species *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) and *Vismia tomentosa* Ruiz & Pav. (Clusiaceae) were selected because of their widespread occurrence.

The upper study site (3000 m a.s.l.; 04°06' S, 79°10' W) was located in the elfin forest close to the timber line in the Podocarpus National Park. This area belonged to the elevated parts of the eastern Cordilleras and was exposed to gusty eastern winds (Richter, 2003). Wind speeds were generally higher than in the montane forest, with mean wind speeds between 4 and 5 m s⁻¹, and maximal values up to 24 m s⁻¹ (M. Richter, pers. comm.). The soils were often waterlogged and characterized by low pH_(CaCl2) between 2.7 and 3.0, deep organic surface layers (average of 0.3 m) and shallow mineral soils (average of 0.4 m). Average bulk densities are listed in Table 1. Slope angles varied from 20° to 50°. At this altitude the tree species *Weinmannia loxensis*

Harling (Cunoniaceae), *Clusia* sp. (Clusiaceae) and *Styrax foveolaria* Perkins (Styracaceae) were selected for measurements.

Measurements

Sampling design

Measurements of root and stem morphology were performed on seven to ten individuals per species (Table 2). Trees were either dominant (i.e. protruding from the canopy) or co-dominant (i.e. reaching the height of the canopy). To record the features that may improve tree anchorage, the entire root ball with all structural roots (defined as roots with a diameter >0.020 m at 1900 m, and >0.015 m at 3000 m, respectively) was excavated within a radius of 0.3 m (1900 m) or 0.2 m (3000 m) around the stem. The minimal root diameter and the radius of the excavation were modified depending on altitude because of the differences in tree size between these two sites.

Spatial arrangement of roots

The depth where structural roots originated from the stem or the tap root, was assigned to the following classes: (i) above soil surface (stilt roots), (ii) within organic surface layer, (iii) at the interface between organic surface layer and mineral soil, (iv) within 0–0.1 m depth, (v) 0.1–0.2 m depth, and (vi) 0.2–0.3 m depth of mineral soil. The cross sectional area was measured separately for all roots growing in a specific soil depth by using the equation:

$$CSA = \pi \cdot \left(\frac{d_h + d_v}{4} \right)^2,$$

where d_h is the horizontal and d_v is the vertical diameter of the respective root, measured with callipers near the stem base after the zone of rapid taper (ZRT; Wilson, 1975).

Root system asymmetry was measured with a technique similar to the one described by Nicoll and Ray (1996). Orientation of taproots at their deepest branching point with structural lateral roots was also included in the measurement, because on slopes, taproots were often not vertically orientated. The horizontal orientation of all structural roots was recorded in two different ways: (a) For the orientation of the root origin the azimuth angle α was measured between the line that is oriented in slope direction and the line

Table 1. Bulk densities at different soil depths at 1900 m and 3000 m a.s.l.

Soil depth [m]	Bulk density [g cm ⁻³]	
	1900 m a.s.l.	3000 m a.s.l.
Upper 0.05 m of forest floor	0.05	0.07
Rest of forest floor	0.09	0.09
0.0–0.1	0.44	0.38
0.1–0.3	0.77	0.93
0.3–0.5	0.81	1.60
0.5–0.7	0.90	1.64

Table 2. Morphological parameters related to tree stability of typical tree species growing at 3000 m and 1900 m a.s.l.

	Extent of root asymmetry R (angle β)	Aspect ratio (m m^{-1})	Ratio of CSA_{root} to tree height ($10^{-3} \text{ m}^2 \text{ m}^{-1}$)	Number of dominant roots	Tree height (m)	Crown diameter (m)	DBH (m)	Ratio of DBH to tree height (10^{-2} mm^{-1})
3000 m a.s.l.								
<i>W. loxensis</i> ($n = 9$)	0.7 ± 0.1^a	1.4 ± 0.1^a	3.5 ± 0.8^a	2.7 ± 0.4^a	4.5 ± 0.3^a	1.2 ± 1.0^a	0.11 ± 0.01^a	2.4 ± 0.1^a
<i>Clusia</i> sp. ($n = 7$)	0.6 ± 0.1^a	1.1 ± 0.1^a	2.8 ± 0.8^a	2.4 ± 0.3^a	3.6 ± 0.3^a	1.0 ± 1.2^a	0.11 ± 0.03^a	2.9 ± 0.7^a
<i>S. foveolaria</i> ($n = 7$)	0.6 ± 0.1^a	1.4 ± 0.2^a	3.2 ± 0.9^a	1.9 ± 0.1^a	4.0 ± 0.6^a	1.2 ± 1.0^a	0.08 ± 0.01^a	2.1 ± 0.2^a
1900 m a.s.l.								
<i>C. revoluta</i> ($n = 10$)	0.3 ± 0.0^{ab}	1.8 ± 0.1^a	6.8 ± 1.2^a	3.5 ± 0.2^a	10.1 ± 0.5^a	4.0 ± 0.5^a	0.23 ± 0.05^a	2.2 ± 0.4^a
<i>V. tomentosa</i> ($n = 8$)	0.4 ± 0.1^b	1.2 ± 0.1^b	7.1 ± 0.8^a	4.0 ± 0.4^a	13.2 ± 0.4^b	5.4 ± 1.0^a	0.17 ± 0.01^a	1.3 ± 0.1^a
<i>G. emarginata</i> ($n = 7$)	0.2 ± 0.0^a	1.6 ± 0.2^{ab}	4.5 ± 0.4^a	3.9 ± 0.3^a	10.2 ± 0.8^a	4.8 ± 0.5^a	0.16 ± 0.01^a	1.6 ± 0.2^a

Values are means \pm standard errors. Different letters indicate significant differences between species within one altitude (by Scheffé-test or H -test; $P < 0.05$).

that connects the point of origin with the center of the stem (Figure 1); (b) For the orientation in which the root had developed, the azimuth angle β was measured between the line that is oriented in slope direction and the line that connects the root at a distance of 0.2 or 0.3 m to the stem with the point of origin of this root (Figure 1). In the case of branching, the weighted center of the emerging daughter roots was estimated. The center of the CSA, which is a measure for the average orientation of roots, has the coordinates

$$X = \sum_{i=1}^n X_i \quad Y = \sum_{i=1}^n Y_i,$$

where the Cartesian coordinates of the i_{th} root ($i = 1 \dots n$) weighted by the CSA are

$$X_i = \left(\frac{\text{CSA}_i}{\text{CSA}_{\text{total}}} \right) \sin \alpha; \quad Y_i = \left(\frac{\text{CSA}_i}{\text{CSA}_{\text{total}}} \right) \cos \alpha$$

or,

$$X_i = \left(\frac{\text{CSA}_i}{\text{CSA}_{\text{total}}} \right) \sin \beta; \quad Y_i = \left(\frac{\text{CSA}_i}{\text{CSA}_{\text{total}}} \right) \cos \beta,$$

where α is the angle of root origin, β is the angle of root growth direction and CSA_i is the cross sectional area of the i_{th} root and $\text{CSA}_{\text{total}}$ is the sum of cross sectional area of all structural roots. For the center of root origin the CSA was assessed directly after the ZRT, as described in the previous section. For the center of root growth direction CSA was assessed at a distance of 0.3 m (1900 m) or 0.2 m (3000 m) from the stem.

The extent of asymmetry R is represented by the distance between the center of root CSA and the origin of the coordinate system. It is a relative value between 0 and 1 that increases when roots cluster in a preferred direction. R is calculated using the equation

$$R = (X^2 + Y^2)^{\frac{1}{2}}.$$

Proportions within roots and stem

To describe the shape of CSA at the root origin close to the stem after the ZRT, aspect ratios (AR) were calculated according to Mickovski and Ennos (2003b):

$$\text{AR} = \frac{d_v}{d_h}.$$

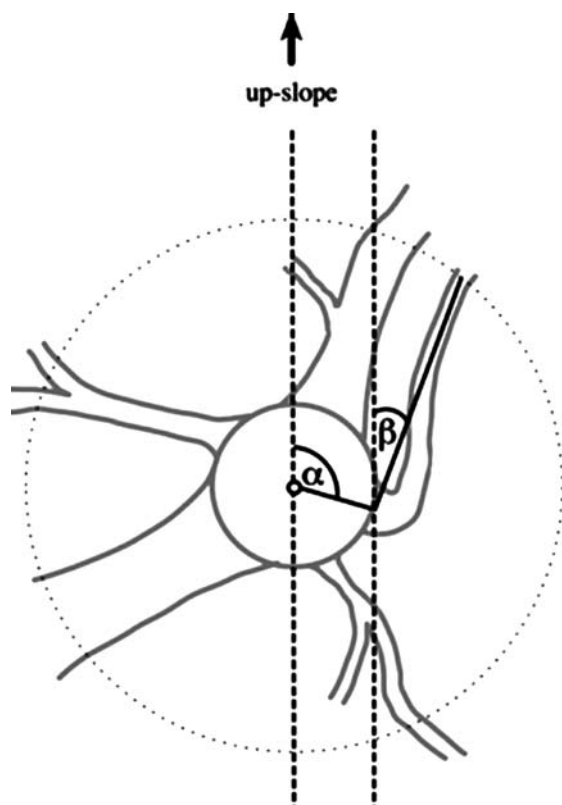


Figure 1. Description of different methods to assess root orientation; angle α : orientation of root origin; angle β : root growth direction; angles were always measured clockwise against up-slope direction (dashed lines); inner circle represents stem cross-section, outer circle (dotted) represents outer limit of root excavation and measuring.

To compare root CSA of trees differing in size, the ratio between root CSA and tree height was calculated. All structural roots were considered for the calculation of the CSA. For every tree the number of dominant roots was recorded. Dominant roots were defined as the largest roots summing up to 80% of total CSA of all structural roots (Coutts et al., 1999).

Other root traits influencing tree stability

The presence or absence of the following qualitative features that were supposed to improve tree stability, were recorded: (a) vertically growing tap roots, (b) stilt roots, (c) support of stem, stem base or coarse roots by stems or coarse roots of neighbouring trees, (d) trees with two or more shoots which were connected by structural rhizomes and (e) I-beam and T-beam shaped roots and other shapes of root CSA.

Shoot characteristics

For every excavated tree several shoot characteristics were determined. Tree height was assessed with a hypsometer (Vertex, Forestor Instruments, Sweden) at 1900 m and a tape measure at 3000 m. Crown diameter was assessed visually by estimating crown radius in four directions with an accuracy of 0.5 m. Additionally, diameter at breast height (DBH) and its relation to stem height was assessed. The inclination of all stems was classified as upright, inclined, lying or partly uprooted (Table 3). When trees were lying or partly uprooted, the length of the stem positioned in or on the forest floor was determined with a tape measure.

Statistical analyses

For the depth of root origin, the extent of root asymmetry R , aspect ratio, the ratio of CSA_{root} to tree height, the number of dominant roots and the stem parameters differences between the two altitudes were assessed using a student's t -test. At 1900 m, the three means of *G. emarginata*, *C. revoluta* and *V. tomentosa*, and at 3000 m, the three means of *W. loxensis*, *Clusia* sp. and *S. foveolaria* were used as replicates for the t -test. For R , aspect ratio, ratio of CSA_{root} to tree height, tree height, crown diameter and ratio of DBH to tree height, one way ANOVA and Scheffé-test for uneven samples sizes were used to assess differences between species within one altitude. For the number of dominant roots and DBH, the non-parametric H -test was used to assess differences between species within one altitude.

Table 3. Classification of stem inclination

Category	Explanation
Upright	Upright to 15° inclination from the vertical
Inclined	> 15° inclination from the vertical
Lying	Lower part of stem lying on soil surface, all structural roots anchoring in soil
Partly uprooted	Lower part of stem lying on soil surface; structural roots partly uprooted

Results

Spatial arrangement of roots

Roots were initiated at a higher position above soil or within soil at 3000 m than at 1900 m (Figure 2). At 1900 m 53% of root CSA derived from roots originating at the interface between forest floor and mineral soil or in the mineral soil. At 3000 m no roots were initiated in mineral soil and 78% were initiated in the forest floor. Stilt roots summed up to 21% of root CSA at this altitude.

At 1900 m, root CSA in the zone of root initiation (angle α) did not cluster in a specific direction as indicated by the uniform distribution of the closed symbols around the center of the diagram in Figure 3a. In contrast, at 3000 m there was conspicuous root clustering in up-slope direction. This is shown by the distribution of the open symbols, which are located mainly in the upper two quadrants in nearly all trees (Figure 3a).

When root CSA was measured further away from stem surface and when orientation of CSA was defined as the direction of root growth (angle β), root clustering became even more distinct (Figure 3b). Roots at 3000 m were markedly clustered in an up-slope direction with a clear deviation to the eastern side. At 1900 m, differences in the orientation of root clustering between species became apparent (Figure 3b). Roots of *C. revoluta* only clustered down-slope, but those of *V. tomentosa* only up-slope. The

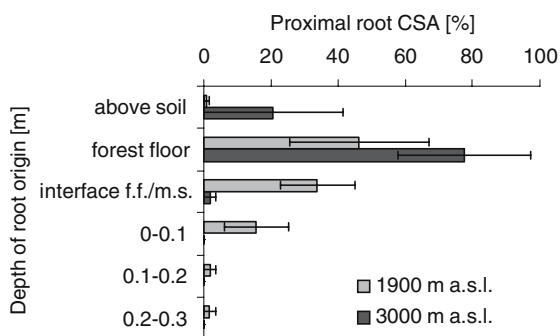


Figure 2. Origin of the lateral roots in trees growing at 1900 m and 3000 m a.s.l. (means and standard errors); f.f. = forest floor, m.s. = mineral soil.

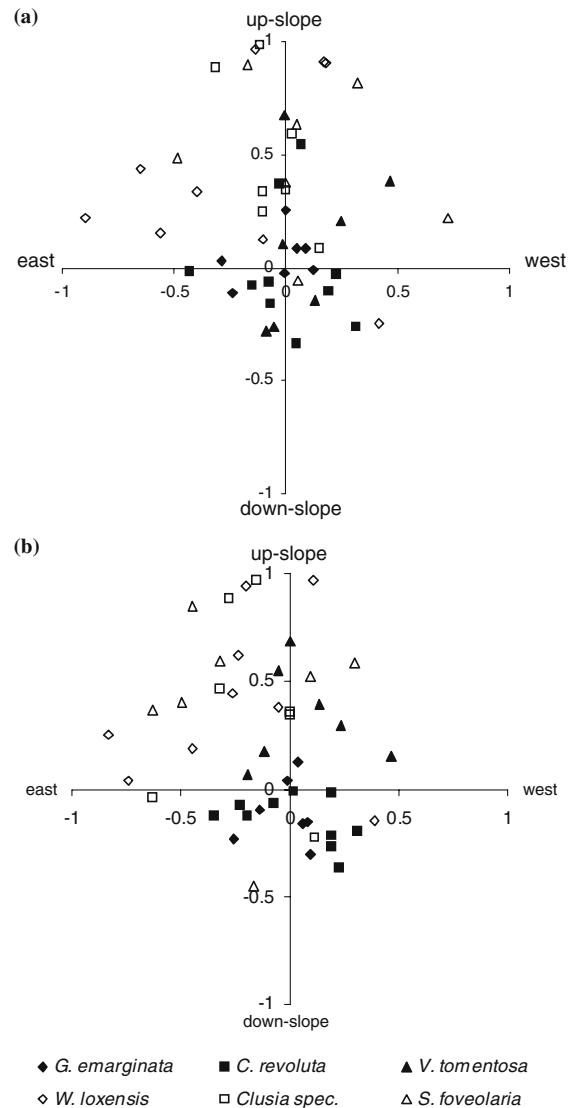


Figure 3. Average orientation of root CSA relative to slope direction; (a) average orientation of root origin, center represents stem center; (b) mean direction of root growth, center represents respective point of origin of every root. Axes show a scale for the extent of asymmetry R . R has a norm of 0 when there is no root clustering and a norm of 1 when 100% of root CSA is orientated in the same direction. Filled symbols: tree species at 1900 m; open symbols: tree species at 3000 m.

root system of *G. emarginata* was oriented down-slope in 5 of 7 trees.

The extent of root asymmetry R was significantly higher ($P = 0.012$; $n = 3$) at 3000 m than at 1900 m. The minimal diameter of roots included in the measurements was 0.020 m at 1900 m and 0.015 m at 3000 m. However, at

3000 m roots with a diameter < 0.020 m contributed less than 3% to the total CSA in 17 of the 23 trees measured. This shows that the effect of altitude on R was not caused by the method of root sampling. R was not correlated with slope gradient (Figure 4a).

Proportions within roots and stem

After the ZRT, structural roots of *Clusia* sp. and *V. tomentosa* had aspect ratios close to 1, i.e. they were nearly circular in cross section (Table 2). Thus, the shape of their root CSA was not influenced by mechanical stress. Roots of *C. revoluta* had the highest aspect ratios, i.e. here, the response to mechanical stress was most pronounced. The formation of small buttresses was typical for this species. Aspect ratios differed significantly between species within 1900 m. There was no effect of altitude on aspect ratio.

In relation to tree height, root CSA was higher at 1900 m than at 3000 m ($P = 0.025$; $n = 3$), i.e. tree anchorage was favored by large ratios of CSA_{root} to tree height at lower altitude. This parameter did not differ significantly

between species within one altitude (Table 2). Tree species at 3000 m had a significantly lower number of dominant roots ($P = 0.006$; $n = 3$) than tree species at 1900 m. There was no consistent difference between species within one altitude (Table 2). None of the parameters aspect ratio, ratio of CSA_{root} to tree height and number of dominant roots was correlated to slope angle (Figure 4b–d).

Qualitative traits of root anatomy

All six species differed markedly in their root architecture (Figure 5). *Clusia* sp. (at 3000 m) was characterized by the development of stilt roots up to 1 m height. Stilt roots were also found on species of *Clusia* at 1900 m, but there they were only initiated close to the base of the trunk. *Clusia* sp. (at 3000 m) and *V. tomentosa* (at 1900 m) were the only species forming tap roots. The vertical extension of taproots, however, was much more limited at 3000 m than at 1900 m (Figure 5). At 3000 m, the taproots penetrated only the organic surface layer. At 1900 m, vertical extension of taproots was impeded at

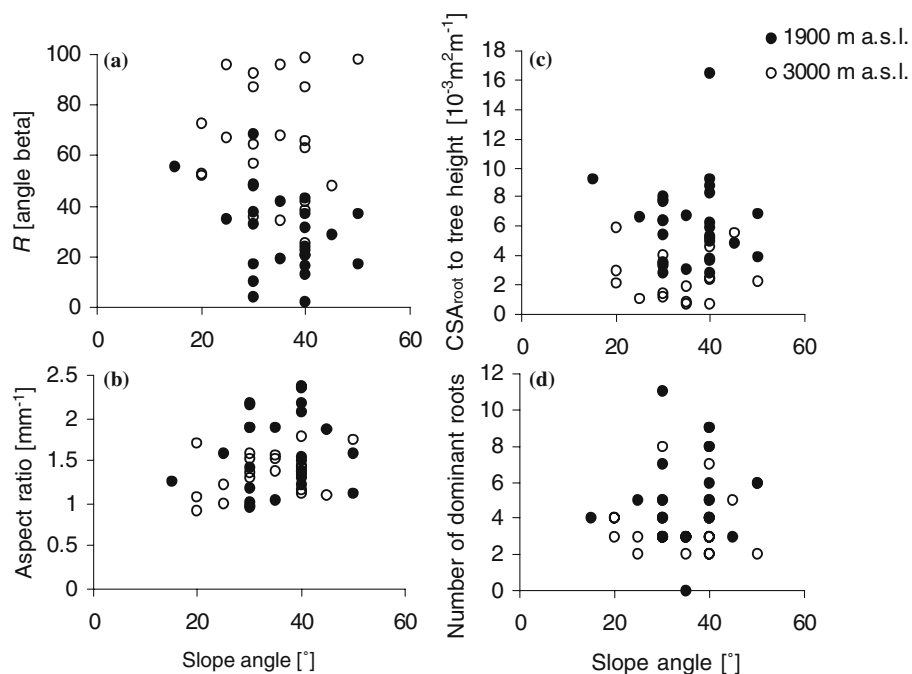


Figure 4. (a) Root asymmetry R (angle β), (b) aspect ratio, (c) ratio of CSA_{root} to tree height and (d) number of dominant roots at 1900 m and 3000 m in relation to slope angle.

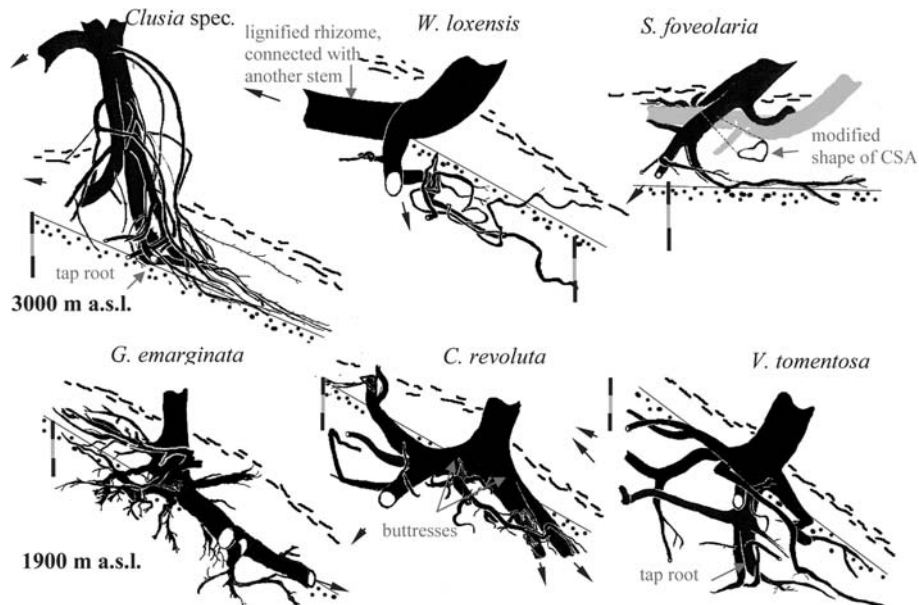


Figure 5. Typical appearance of coarse root systems of the investigated tree species, derived from photographs; black arrow = skeleton root continues; gray figure = stem of other tree; dots = surface of mineral soil; dashed lines = surface of forest floor; scale sections = 0.1 m.

depths of about 0.5–0.8 m in the mineral soil. Thus, all tap roots changed growth direction at certain soil depths. *W. loxensis* (at 3000 m) was the only species that had the ability to propagate by rhizomes, i.e. creeping underground stems with the ability to produce new shoots (Figure 5). Up to three shoots were connected by large structural rhizomes. Since the root systems were not completely excavated horizontally, it can be expected that even more shoots belonged to one plant.

The CSA of structural roots near the stem of *S. foveolaria* (at 3000 m) and *C. revoluta* (at 1900 m) often deviated clearly from a circle. For *C. revoluta*, this has already been shown by the aspect ratio (Table 2). Buttresses were often I- and T-beam shaped. Eccentric root CSA with typical I- and T-beam shapes were rarely found in *S. foveolaria*. The shape of CSA of this species was especially modified at the locations where the stem base was supported by roots of other trees, increasing the contact area between stem base and root (Figure 5).

Root systems of *G. emarginata* growing at 1900 m were characterized by vertically growing laterals similar to sinker roots (Figure 5). High branching frequencies resulted in a relatively

small root system radius and thus in small horizontal extension of the potential root–soil plate.

Shoot characteristics

Tree height, crown diameter and DBH were significantly higher at 1900 m than at 3000 m ($P = 0.002$, $P = 0.001$ and $P = 0.020$, respectively; $n = 3$). Ratios of DBH to tree height were slightly, but not significantly higher at 3000 m, i.e. at this altitude, trees had higher stem taper (Table 2). At both altitudes stem inclination was oriented in down-slope direction, but there were marked differences in the extent of inclination between altitudes. At 1900 m 92% of trees grew upright or slightly inclined (Figure 6a), in comparison with 52% at 3000 m (Figure 6b). At 3000 m 48% of trees were inclined, lying or partly uprooted. Between 0.3 m and 0.8 m of the stem were positioned within or on forest floor when trees were lying or partly uprooted. At this altitude most trees grew upright when shoots were connected by rhizomes or in the presence of taproots or stilt roots (Figure 7). In contrast, most trees with roots showing either modifications of the CSA or no special root feature were lying or even partly uprooted (Figure 7).

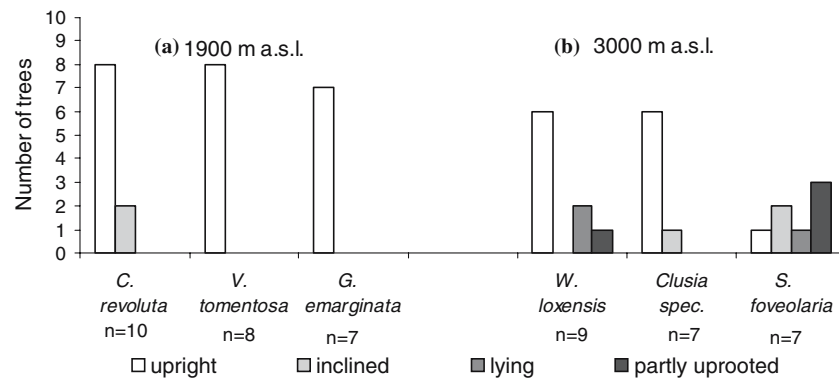


Figure 6. Appearance of tree stems with respect to tree rigidity at (a) 1900 m and (b) 3000 m; n = number of trees of the respective species.

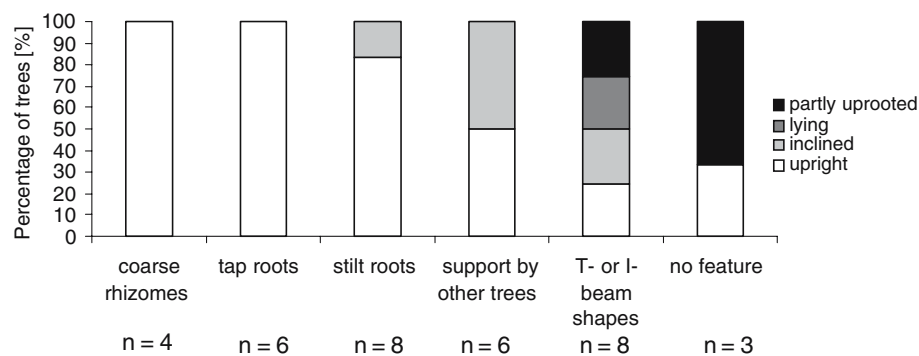


Figure 7. Relationship between the occurrence of a specific root trait (coarse rhizomes, tap roots, stilt roots, support by other trees, T- or I-beam shapes of root cross sections, no specific trait) and tree rigidity as assessed by the percentage of trees in different classes of stem inclination (upright, inclined, lying, partly uprooted) for trees growing at 3000 m; n = number of trees showing specific root traits.

Discussion

Importance of the observed morphological root traits for tree anchorage

In the montane and elfin forest of Southern Ecuador, a variety of root traits were observed that improve tree anchorage in soil. The extent of root asymmetry R with respect to both the direction of root origin and the direction of root growth at both altitudes was higher than in a study on Sitka spruce (*Picea sitchensis* Bong. Carr.) trees growing on slopes $\leq 14^\circ$ (Nicoll and Ray, 1996). In the elfin forest, the extent of root asymmetry was higher than in a study on *Pinus peuce* (Mickovski and Ennos, 2003b). Root asymmetry influences root system stiffness in different directions. For example, winching stems of

mature Sitka spruce sideways resulted in tree failure in the directions where main roots were less well developed (Coutts, 1983). Thus, root asymmetry is important for tree stability when mechanical forces e.g. wind loading are not evenly distributed around the stem.

Root asymmetry and root clustering can also be caused by physical obstructions of roots or the spatial variability of water and nutrient availability in soil (Coutts et al., 1999; Mickovski and Ennos, 2002). The occurrence of root clustering in the eastward up-slope direction in the elfin forest (Figure 3b) was accompanied by eastern winds, while root clustering in either up-slope or down-slope direction in the montane forest was accompanied by mountain and valley winds. This indicates that root asymmetry in the present study was mainly caused by mechanical loads

and reflects the importance of horizontally growing roots for tree anchorage in shallow but also in deeper soils. However, this study does not allow to quantify the contribution of wind loading and “self loading” on root system asymmetry. It can be assumed that at 3000 m the gusty winds have a major impact on root system asymmetry while at 1900 m “self loading” forces get more important because of lower wind speeds and higher biomass of the trees.

The main direction of mechanical forces was related to the direction of root growth (Figure 3b) rather than to the orientation of root origin (Figure 3a). This indicates that roots reoriented, e.g. as a result of soil creeping or tree movement, or that some roots tapered or died and new branches formed in a different direction. According to our observations reorientation of roots was a very common feature. Thus, it is also possible that in several cases root asymmetry is a result of tree or soil movement rather than a mechanism to improve tree stability.

Buttresses as well as I- and T-beam shapes were most pronounced in *C. revoluta*, i.e. the species with the most superficial root system at 1900 m. The formation of buttresses or cross sections with an I- or T-beam shape may further improve anchorage by maximizing the bending resistance of the roots with a minimum of biomass costs (Coutts et al., 1999; Mattheck, 1992). For example, anchorage strength of buttressed tree species of the tropical lowlands was almost doubled in comparison to unbuttressed species (Crook et al., 1997). These modifications in the shape of root cross sections are usually found in superficial roots or root systems (Mickovski and Ennos, 2003b; Nicoll and Ray, 1996). In contrast to *C. revoluta*, structural roots of *V. tomentosa* and *Clusia* sp. were nearly circular in cross section. In these two species, horizontally growing roots were less important for tree stability because of the presence of taproots and stilt roots. Tap roots moderate external forces by shifting the hinge point from the soil surface to deeper soil zones (Polomski and Kuhn, 2001). Together with windward sinkers they contributed to 75% of anchorage strength in *Larix* sp. (Crook and Ennos, 1996). The functioning of stilt roots is similar to a guy rope, increasing the lever arm lateral to the stem (Mattheck, 1992). Results from the present study support the

assumption that modifications in root cross sections are most pronounced in the absence of other root traits that improve tree stability.

In the present study the impact of these root traits on tree rigidity was not measured. Rather, their effectiveness to improve anchorage was estimated by stem inclination. The uniform direction of stem inclination shows that inclination is the result of mechanical loadings acting on the trees. Inclination of stems at 3000 m suggests that taproots, stilt roots and rhizomes enabled trees to resist mechanical forces (Figure 7). In contrast, inclination of trees with the formation of I- and T-beam shaped root CSA suggest that this trait was not sufficient to prevent stem inclination in the elfin forest. However, information is lacking on the time of the formation of these root traits. It is possible that in several cases I- and T-beam shaped root CSA formed after stem inclination.

Site specific differences in root and stem morphology

Even though root traits related to plant anchorage were often species specific, root system architecture was also significantly influenced by the different environmental conditions prevailing at different altitudes. Altitudes differed in wind speed and soil conditions, while slope angles were comparable. There was no correlation between slope angle and the extent of any root trait related to tree anchorage, suggesting that the extent of these traits is governed by other factors such as heterogeneities in wind loadings or the weight of the tree. The results of this study are in contrast to the results of Di Iorio et al. (2005) who found higher numbers of first order roots and lower basal CSA as well as lower extents of root asymmetry in *Quercus pubescens* Willd. and *Quercus cerris* L. trees growing on shallow slopes (4°–5°) than growing on steep slopes (14°–34°). The authors explained the impact of slope angles on root morphology by higher turning moments acting on the shoot on steep slopes.

Rooting depth affects the vertical extension of the root soil plate. In contrast to 3000 m, at 1900 m many structural roots originated in the mineral soil (Figure 2) which had higher bulk densities (Table 1) and thus provided more stability than the forest floor. In comparison to 3000 m, at 1900 m dissipation of forces to

mineral soil was further improved by the presence of rigid main tap roots in *V. tomentosa* and by vertically growing lateral roots similar to sinkers in *G. emarginata* (Figure 5). Thus, at this altitude the vertical extension of the root–soil plate may be of special importance for anchorage. The restriction of root origin to the forest floor at 3000 m (Figure 2) was accompanied by poor development of taproots of *Clusia* sp. in comparison to good tap root development of *V. tomentosa* growing at 1900 m (Figure 5). The final extension of taproots and root systems in general is strongly influenced by soil conditions and groundwater level (Cucchi et al., 2004; Kodrik and Kodrik, 2002; Rigg and Harrar, 1931). Investigations on the effect of vertical root growth restriction on anchorage strength led to contradictory results (Cucchi et al., 2004; Schaetzl et al., 1989). In the present study, vertical root extension at 3000 m was possibly restricted by waterlogged and shallow mineral soils (Schrumph et al., 2001). As the bulk density in the forest floor is low, the concentration of root growth to the forest floor at 3000 m is expected to reduce tree stability (Ray and Nicoll, 1998; Rigg and Harrar, 1931).

Several root traits were supposed to have an impact on the horizontal extension of the root–soil plate. At 1900 m strains might be transmitted to the soil closer to the stem than at 3000 m because of a larger root surface area (Ennos, 1990). A relatively larger root surface area at 1900 m is derived from higher ratios of CSA_{root} to tree height and higher numbers of dominant roots (Table 2) as well as high branching frequencies near the stem in *G. emarginata* (Figure 5). When trees have little anchorage from deeper growing roots, the horizontal extension of the root–soil plate becomes more important for tree anchorage (Cucchi et al., 2004; Mickovski and Ennos, 2003b). In accordance to this, the extent of root system asymmetry R was significantly higher in the elfin forest than in the montane forest (Table 2). The high extent of root system asymmetry in the elfin forest was accompanied by small numbers of dominant roots at this site (Table 2). Dominant roots, i.e. the largest roots summing up to 80% of total CSA, are considered to be the most relevant roots for plant anchorage, because the stiffness of roots increases with the fourth power of their diameter

(Coutts et al., 1999). The distribution of 80% of total root CSA to a lower number of dominant roots may be regarded as the optimum investment of biomass with respect to rigidity (Coutts, 1983).

Another very effective trait to improve the horizontal extension of the root–soil plate and thus tree stability is the propagation of *W. loxensis* by lignified rhizomes (Figure 7). It is possible that this trait results in a marked resistance to uprooting and that it is one reason for the high abundance of this species in the elfin forest. Support of the stem base or roots, either by nurse logs or by aboveground parts of the trees also occurred quite frequently in the elfin forest but was never observed in the montane forest. The development of trees on fallen logs or wood fragments is a typical feature of tropical montane forests with waterlogged soils and can be explained by a more favorable oxidation–reduction potential in these locations than in the underlying soil horizons (Santiago, 2000). In the present study, this mutual support was always accompanied by upright or just inclined stems (Figure 7). In combination with the high coarse root density support of the stem base or roots might be an important factor for tree stability at this site, because the low bulk density of the forest floor reduces its function as a hard bearing subsurface (Stokes and Mattheck, 1996). Furthermore, contact between roots and stems of neighbouring trees might improve anchorage by damping the effect of swaying due to high wind speeds. This damping effect was also found to be a function of crowns being in contact with each other in dense stands (Cucchi and Bert, 2003).

Besides root morphology above ground tree architecture also differed between altitudes (Table 2). Shorter stems with smaller crown areas in the elfin forest in comparison with the montane forest reduce wind induced turning moments (Nielsen, 1990) and may be thigmomorphogenetic responses to high wind speeds (Cordero, 1999). Higher taper of stems in the elfin forest causes more resistance to bending (Moore, 2000) and is another typical adaptation to high wind speeds (Lawton, 1982). This elfin tree stature may reduce wind loadings on the root systems enabling trees to grow on the shallow soils of this site.

In conclusion, native tree species growing on steep slopes of a south Ecuadorian tropical

montane and elfin forest showed a variety of root traits related to plant stability. These traits were both species and site specific, but were not related to slope angle. Generally, mechanical loads caused a marked root asymmetry in these forests. Root traits improving the horizontal extension of the potential root–soil plate became even more important in higher altitudes, where deep rooting was markedly impeded by soil properties. Furthermore, high coarse root densities and mutual support of roots and stems seemed to improve tree rigidity in elfin forests where bulk densities of the rooted soil horizons were low and wind speeds were high.

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