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# Worldwide hemisphere-dependent lean in Cook pines

Under most conditions, trees grow vertically in response to the opposing influences of light and gravity (Wyatt and Kiss 2013). In challenging environments, where competition for light or mechanical stress is intense, trees may grow non-vertically (Loehle 1986). Here we describe a novel hemisphere-dependent leaning habit in *Araucaria columnaris* (Cook pine) (J.R. Forst.), a widely cultivated conifer endemic to New Caledonia. Specifically, in a large sample of individuals from around the world, we demonstrate that the Cook pines' lean is non-random: trees in the northern hemisphere lean south, and those in the southern hemisphere lean north. Additionally, the magnitude of the lean is more pronounced at higher latitudes in both hemispheres. Our data and the pattern that we describe here elucidate the fact that plants are responding to their global environment in a way not yet fully understood.

A tree's form is determined by the complex interactions of genetics and environmental stimuli (Braam 2005). Under most conditions, trees grow vertically in response to the opposing influences of light and gravity (Loehle 1986). In challenging environments, where competition for light or mechanical stress is intense, trees may grow in a non-vertical fashion (Braam 2005, Telewski 2006). Although the growth responses contributing to vertical growth have been studied for over 100 yr, the mechanisms driving them remain only partly elucidated (Darwin and Darwin 1880, Sinnott 1952, Wyatt and Kiss 2013). Never before has a hemisphere-dependent leaning pattern been documented across a tree species.

*Araucaria columnaris* (J.R. Forst.) Hooker, the Cook pine, is a New Caledonian endemic conifer, which has been planted in temperate, subtropical, and tropical areas throughout the world (Fig. 1; Kershaw and Wagstaff 2009). When grown outside of its native range, this species has a pronounced lean so ubiquitous that it is often used as the identifying characteristic for the species (Farjon and Filer 2013). While the common lean of *A. columnaris* has been anecdotally observed, its hemisphere-dependent leaning pattern has not been described in the literature. We first noticed *A. columnaris* leaning south in California and Hawaii, where it is a common horticultural plant. Our observation from Australia, though, suggested that *A. columnaris* lean north in the southern hemisphere.

We measured 256 trees on five continents in 18 different regions (distinct areas more than 500 km from each other), spanning 7°–35° N and 12°–42° S latitude, including the species' native range in New Caledonia (21° S). For each tree, we recorded height, trunk diameter at 1.5 m above ground, azimuth direction of lean, and the extent of lean (see Appendix S1). We defined the extent of lean as the horizontal distance on the ground from directly beneath the apical meristem to the base of the trunk. The magnitude of lean is the extent of the lean divided by the tree's height (Appendix S1). We used magnitude of lean for downstream analyses. The median lean for all trees measured is 2.42 m away from the base, and the median tree height is 18 m, resulting in an 8.05° lean angle (95% CI 7.50°–8.50°).

We uncovered a surprisingly consistent pattern of hemisphere-dependent directional leaning in *A. columnaris*. In the northern hemisphere, trees lean south (median azimuth of 151°, 95% CI 144°157°), and in the southern hemisphere they lean north (median azimuth of 0°, 95% CI −15°10°; Fig. 2). Fewer than 9% of individual trees lean away from their predicted direction. This pattern is consistent across all regional samples (18/18; sign test, $P << 0.001$).

We also examined the relationship between magnitude of lean and latitude (Fig. 3). For these analyses, we used

Fig. 1. Typical cultivated stand of *Araucaria columnaris* at the University of California, Irvine campus (33.65° N, 117.84° W; Irvine, California, USA).

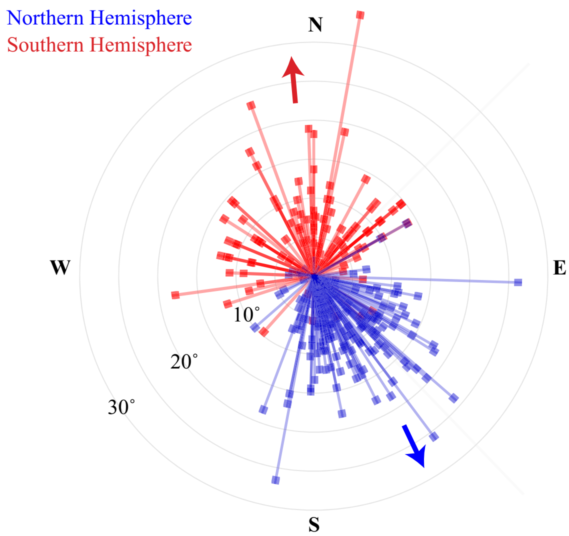


FIG. 2. Hemisphere-dependent magnitude and azimuth of lean for each measured tree ($n$ = 256). The circular position of each point gives the compass azimuth. Cardinal directions are marked. The magnitude of lean is given by lines radiating from the center and measured in degrees from vertical, as indicated by concentric circles. Red points represent samples from the southern hemisphere, and blue points those from northern hemisphere. Arrows indicate mean azimuth of lean for trees in each hemisphere.

only the north-south axis component (scalar) of lean azimuth, or "axial lean" (Appendix S1). We found that a simple linear regression explains 54% of the variance, suggesting that trees lean more the further they are from the equator ($R^2$ = 0.543, $F_{1,254}$ = 304.4, $P$ << 0.001).

The cause of directional lean in this species is unclear. Vertical growth in shoots is generally maintained by a negative relationship with gravity (negative gravitropism; Hashiguchi et al. 2013) and a positive relationship with their light source (positive phototropism; Darwin and Darwin 1880, Loehle 1986, Christie and Murphy 2013). Non-vertical shoot growth can be caused by mechanical perturbation from wind or snow or by a phototropic response to a light source that is not directly above the shoot (Tomlinson 1983, Telewski 2006). Mechanistic studies in *Arabidopsis thaliana* have identified several gene families whose regulation effects phototropic and gravitropic growth in plants. However, the mechanisms controlling the expression of these genes and the interactions between them are not well understood, especially for woody species (Wyatt and Kiss 2013).

The leading hypothesis for the molecular mechanism of gravitropism is that sedimentation of amyloplasts on actin microfilaments activates a signal transduction pathway resulting in asymmetric transport of auxin in the stem, causing it to straighten itself parallel with the gravity vector (Hashiguchi et al. 2013). This hypothesis, like phototropism, is supported by the identification of genes whose proper expression is necessary for observing a gravitropic phenotype.

Phototropism acts principally during primary growth in shoot tips to maintain an upright form in trees (Speck and Burgert 2011). Once secondary growth begins in stems, trees correct asymmetrical growth by forming reaction wood (Sinnott 1952, Du and Yamamoto 2007). Reaction wood results from asymmetric growth in the vascular cambium and can cause a leaning stem to correct itself to vertical. Although the mechanisms are different in gymnosperms (compression wood) and angiosperms (tension wood), trees can reestablish vertical growth after external forces cause leaning (Plomion et al. 2001).

The mechanisms underlying directional lean of *Araucaria columnaris* may be related to an adaptive tropic response to the incidence angles of annual sunlight, gravity, magnetism, or any combination of these (Loehle 1986, Christie and Murphy 2013). It is interesting that the pronounced lean in *A. columnaris* is rare in other species, including other *Araucaria* native to New Caledonia. It is possible that the biophysical constraints of

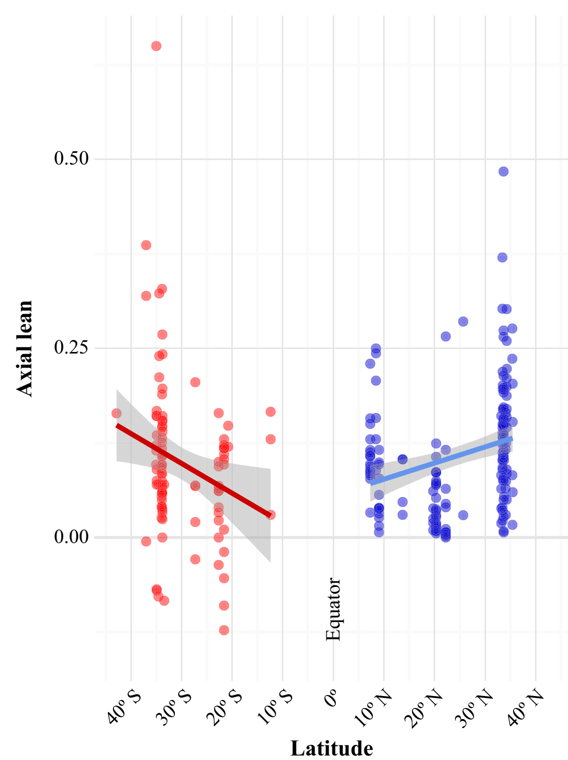


FIG. 3. Axial lean vs. latitude ($n$ = 256). Axial lean gives a measure north-south component lean. It is calculated as the magnitude of lean multiplied by the cosine of the lean azimuth. Latitude is a strong predictor of axial lean ($R^2$ = 0.543, $F_{1,254}$ = 304.4, $P$ << 0.001). For clarity, we show the absolute value of axial lean separated for each hemisphere, so that increasing values indicate greater axial lean away from the equator.

leaning for a tall tree ultimately prevail over any benefits of additional light interception gained by leaning (Read and Stokes 2006). Another possibility is that the lean is non-adaptive, or even harmful. Even though *A. columnaris* is one of the most widespread *Araucaria* species in New Caledonia, and the only one to express a lean, the species may nevertheless have small effective population sizes, and suffer fixation of deleterious alleles.

Regardless of which causal processes give *A. columnaris* its characteristic lean, this unique phenomenon needs further study. A better understanding of the dramatic leaning pattern in this species may lead to discoveries regarding the underlying mechanisms linking plant responses to environmental cues.


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## Literature Cited


Braam, J. 2005. In touch: plant responses to mechanical stimuli. New Phytologist 165:373–389.

Christie, J. M., and A. S. Murphy. 2013. Shoot phototropism in higher plants: new light through old concepts. American Journal of Botany 100:35–46.

Darwin, C., and F. Darwin. 1880. The power of movement in plants. Appleton, London, UK.

Du, S., and F. Yamamoto. 2007. An overview of the biology of reaction wood formation. Journal of Integrative Plant Biology 49:131–143.

Farjon, A., and D. Filer. 2013. An atlas of the world's conifers: an analysis of their distribution, biogeography, diversity and conservation status. Brill, Leiden, The Netherlands.

Hashiguchi, Y., M. Tasaka, and M. T. Morita. 2013. Mechanism of higher plant gravity sensing. American Journal of Botany 100:91–100.

Kershaw, P., and B. Wagstaff. 2009. The southern conifer family Araucariaceae: History, status, and value for paleoenvironmental reconstruction. Ecology 32:397–414.

Loehle, C. 1986. Phototropism of whole trees: effects of habitat and growth form. American Midland Naturalist 116:190–196.

Plomion, C., G. Leprovost, and A. Stokes. 2001. Wood formation in trees. Plant Physiology 127:1513–1523.

Read, J., and A. Stokes. 2006. Plant biomechanics in an ecological context. American Journal of Botany 93:1546–1565.

Sinnott, E. W. 1952. Reaction wood and the regulation of tree form. American Journal of Botany 39:69–78.

Speck, T., and I. Burgert. 2011. Plant stems: functional design and mechanics. Annual Review of Materials Research 41:169–193.

Telewski, F. W. 2006. A unified hypothesis of mechanoperception in plants. American Journal of Botany 93:1466–1476.

Tomlinson, P. B. 1983. Tree Architecture: New approaches help to define the elusive biological property of tree form. American Scientist 71:141–149.

Wyatt, S. E., and J. Z. Kiss. 2013. Plant tropisms: From Darwin to the international space station. American Journal of Botany 100:1–3.



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