The adaptive significance of trunk inclination on slopes: a commentary

CRAIG LOEHLE

Environmental Research Division, Argonne National Laboratory, Argonne, IL 60439, USA

SUMMARY

A recent study explored the adaptive significance of trunk inclination for trees growing on steep slopes. The authors used an optimality argument to predict how much a tree should respond to sidelight. Their calculations of the costs of leaning are flawed, because: (i) leaf mass has an allometric relationship with total volume, rather than being a fixed proportion of wood mass; (ii) the cost of support wood tissue is mainly a growth rate cost, not a maintenance respiration cost; (iii) small trees are sufficiently elastic to need very little support tissue, and thus they have a different risk structure; and (iv) most crown gaps are ephemeral rather than permanent, which also changes the risk equation. The argument I proposed in a previous study, addressing exactly the same question, is that canopy species are under selective pressure to maintain a strong central trunk that will reach the canopy and thus should not respond to sidelight. A reproductive value model is presented to illustrate this evolutionary question. Small, short-lived species or those from habitats with permanent openings (such as river margins) should be responsive. Both my previous data and the data of the other study support my model, but the model in the other study leaves many facts unexplained.

A recent paper in this journal (Ishii & Higashi 1997) addressed the adaptive significance of trunk inclination on slopes relative to light regimes. Unfortunately, some fundamental errors affect their conclusions. The relationship they use for green mass relative to wood mass is incorrect, their calculation of increased mortality due to leaning was based on an incorrect calculation of a respiration effect, they failed to consider the difference in wood properties between small and large trees, the reason they gave for the lack of response by shade-tolerant trees to sidelight was incorrect, and the ephemeral nature of most gaps was ignored. Furthermore, as I showed previously (Loehle 1986), some shade-intolerant species do not respond to sidelight.

I will briefly recapitulate Ishii & Higashi's arguments, then show that a more coherent argument about trunk inclination can be made. Observing that some trees will grow into openings in the forest or incline their trunks at forest edges, we can ask how much these trees should lean under different conditions. They took a cost–benefit approach, which is valid for questions of adaptation if costs and benefits are tallied correctly.

The benefit to leaning on a hillside is assumed by Ishii & Higashi to be a closer approach to the canopy and therefore to light. The increased light increases photosynthesis, providing a net benefit to the tree. This is a basically correct argument. We note, however, that trees lean in locations besides steep slopes, including swamps, river margins, forest edges, and

the forest understory on flat terrain. We may consider, under these various conditions including on slopes, that trees are responding to light rather than to the slope *per se*, since there is no sensory modality by which a tree can detect the angle of slope on which it resides. Asymmetric light regimes may therefore be considered to be the common characteristic of these various situations. To properly assess leaning under these various conditions, we must consider the permanence of openings. The model of Ishii & Higashi implicitly assumes a permanent advantage for a tree that grows at an angle. In many cases, however, sidelight is only temporary, a situation whose evolutionary implications I explore below. Here we may simply note that if sidelight conditions are ephemeral, then the advantage (benefit) of growing at an angle depends on the gap duration relative to tree growth rate and life span.

The basic computation of photosynthetic rate in their model is flawed. They assume that crown (green) mass is a constant fraction of trunk mass (their equation 6). However, this is not correct. Leaf biomass typically scales allometrically with total plant mass as:

$$Y = aX^b, \quad (1)$$

where Y is leaf mass and X is total plant mass (Strauss & Ledig 1985). The coefficient b is less than one, making leaf mass a smaller percentage of total mass as the tree gets larger. This throws off the rest of their calculations.

The costs computed by Ishii & Higashi are even more problematic. The first cost they computed is the cost of increased respiration resulting from increased support tissues. The authors estimated the volume of extra support tissue in terms of the volume of columnar trunk that must be supported by the base. The extra support tissue is assumed to be in terms of buckling under the tree's own weight under the assumption of no elasticity. The assumption of no elasticity, however, is invalid for small trees. The natural elasticity of wood permits quite long leaning stems to forego additional support tissue if the weight supported at the end is not large. Bamboo, the ultimate example, can lean and bend outward quite far without breaking and flexes readily in the wind. Thus, for small stems, leaning has almost no cost. As a tree gets larger, however, the wood must become rigid to support the tree's weight. We must therefore distinguish between small and large trees in the analysis of costs. In the absence of consideration of elasticity, their cost model applies only to larger trees, and specifically not to the two understory trees in their study. Even without elasticity, their model predicts very little or no support tissue for small trees, which reduces costs for small trees and should mean that all small trees will lean, which is not the case with their data set.

A final, critical error in the assessment of costs by Ishii & Higashi concerns the respiration costs of the extra support tissue. Even for a large tree with extra support tissue, assessing costs in terms of respiration is not valid, because most stem wood is dead and has no respiratory (maintenance) cost. Instead, production of these tissues occurs at the expense of growth. That is, a tree growing at an angle must grow relatively slowly because part of its photosynthate is diverted to the support tissue. Once the tree reaches its full height, however, and is producing seed, there is little excess respiratory cost. At this point, we must consider competition and gap duration. A tree attempting to grow at an angle into a gap will grow more slowly than a competitor growing in the gap and also must attain greater stem length to reach a given height. (At a 30° angle, a stem must be 35 m long to reach a 30 m canopy height.) In closed forest, a gap will eventually close, either from below or from the sides, and overstory trees must reach the canopy to persist. Thus, overstory trees should not lean unless they can achieve a relatively permanent advantage.

The proper consideration of the evolution of traits requires a fitness argument. Fitness has two components: survival and reproduction. Ishii & Higashi consider only mortality risk as a function of leaning. For a tree, we must consider reproduction over a prolonged period. We may consider as the simplest case an open grown, dominant tree, with height growth governed by

$$dh/dt = g - lh_t \quad (2)$$

where g is the seedling nominal height growth rate ($= 1 \text{ m yr}^{-1}$) and l is a cost to growth due to increased respiratory load with size. With this model, tree height increases at a decreasing rate with age, eventually leveling off at a height of 40 m after 100 years when $l = 0.025$. This height-age curve closely matches real

growth curves exhibited by many fast-growing trees (Oliver & Larson 1996). We may assume a random mortality rate that yields a longevity exceeding 300 years, to obtain a survivorship curve:

$$S_t = (1.0 - c)^t, \quad (3)$$

where c is yearly probability of mortality ($c = 0.01$ here). Seed dispersal distance limits tree reproduction (once saturated with seed, a spot near the tree can not produce further successful offspring). For a tree with wind-dispersed seed, the area reached by seed is typically some multiple, m , of tree height. Then reproductive benefit is proportional to height:

$$R \propto \pi(mh)^2, \quad (4)$$

or collapsing parameters:

$$R = rh^2. \quad (5)$$

The reproductive value at each age (which is not fitness but can be used to find fitness) is simply the reproduction at each age multiplied by the survivorship at that age (assuming that seeds find reproduction opportunities randomly over time):

$$V_t = R_t S_t = rh_t^2 (1.0 - c)^t. \quad (6)$$

This curve rises to a peak at age 69, and then falls because older trees become less likely to survive long enough to reproduce (figure 1).

We may address the cost of leaning qualitatively as follows. Assume that a shift in carbon to support tissue increases l slightly to 0.03 (a more robust lower trunk requires a continuing input of increased annual wood deposition to maintain conducting tissues). For a tree growing at 30° off the vertical, the height from which seed are dispersed is now $\sin(60)h = 0.87h$, so the new V is:

$$V_t = r(0.87h_t)^2 (1.0 - c)^t, \quad (7)$$

with the height-age curve (equation (2)) now being computed with the larger l value. This produces a lower curve at all ages (figure 1) and a peak at a younger age (63) than before. There is thus a much higher reproductive value to the tree that does not lean under full sun conditions, so we should not see trees in full sun leaning, and we rarely do. We may also note that the increase in photosynthetic rate due to leaning into a better light zone must be at least enough to compensate for the lost reproductive value resulting from slower growth and a shorter seed dispersal height at any given age. Ephemeral gaps will tend to truncate the right side of the curve unless the tree has reached a given height (and occupied the gap) before the time of gap closure, putting an even stronger selective pressure on trees to not lean unless they can achieve a sufficiently high growth advantage thereby, which generally applies to shade intolerant trees, or have a short life span. Note that in my model the costs of leaning apply even to short trees, though greater costs accrue to taller trees. In this general argument, I do not attempt to model photosynthesis or gap dynamics mechanistically, but rather attempt to show how the time component of growth and mortality interact with reproduction in a

Figure 1. Reproductive value over time for open-grown trees that are straight or leaning.

critical way to produce selective pressures on growth traits. A more complete model would also consider the impact of slowed growth on mortality, which Ishii & Higashi tried to do but with incorrect cost figures. However, to properly consider slowed growth risks to mortality, one must model a tree in competition with other trees. An open grown tree has such good growth that it can tolerate considerable reductions in growth rate without any increased risk of mortality until it is quite old.

From this basic argument (here formalized for the first time), I predicted (Loehle 1986) which species should lean in response to asymmetric light and which should not, then tested the prediction with data from the south eastern United States. A group of five lowland (wet-habitat) species showed much more leaning at forest edges ($\bar{x} = 21^\circ$ from vertical) than the three upland species sampled, which showed almost no leaning ($\bar{x} = 6.61^\circ$ from vertical). This observation is easily explained. In bottomland habitats, a significant fraction of the total area is permanent edges, along rivers and ponds/swamps. A tree leaning over a river cannot be overtopped and need not (and typically does not) grow to a great height. Even when leaning increases the risk of toppling, the rapid growth rate of bottomland species means that a tree leaning over a river produces plenty of seed, and thus offspring, before it topples.

In contrast, upland species face ephemeral gaps and can reach the canopy only by growing nearly straight up. Upland species must thus become canopy dominants or codominants to reproduce successfully (Harper & White 1974). In the Ishii & Higashi study, the dominant overstory species, *Distylium vacemosum*, an upland species, exhibits only modest leaning that is unrelated to hill slope angle. Their model would seem to suggest that this species should lean, but my model predicts that an overstory dominant of closed forest (not a river edge species) should not lean, and thus fits their data.

If a species is small and short-lived, as many understory and forest edge species are, then growth into a gap, even an ephemeral gap, is advantageous, because a small tree might have very little increase in cost due to leaning and can reach full adult size even

in a small gap and before the gap closes from above. This case matches the Ishii & Higashi data on the understory species *Rhododendron tashiroe*, which exhibits increasing leaning with increasing slope. We note the extreme elasticity of *Rhododendron* stems, which bend very far before breaking. Such a wood type is ideal for a small tree that often grows at extreme angles. Thus the only species which they show to be prone to leaning (*Rhododendron*) is one in which there are likely no costs to leaning because of small size, and which thus cannot be explained by their model. In contrast, the overstory species, *Distylium vacemosum*, in their study does not lean. Shade-tolerant species are argued by Ishii & Higashi to be less likely to respond to sidelight, but their sample of one understory shade-tolerant tree that does not lean does not provide sufficient evidence to test this idea. Many shade-tolerant trees are functionally canopy species, reproducing only if they reach a dominant position. Detailed studies of stand dynamics (e.g. Oliver & Larson 1996) indicate that such species show episodic growth as they work their way up into the canopy. These species should show little response to sidelight, and many such species have very straight trunks. This lack of responsiveness is thus not necessarily due to shade tolerance per se. Many small shade-tolerant species (e.g. *Cornus florida*, *Morus rubra*, *Cercis canadensis*), on the other hand, are usually short-lived and are nearly as responsive to sidelight as *Rhododendron*.

An important category of trees that must be considered is emergent species, which tower over the main forest canopy at heights of 60 m or more. Such heights are reached only with strong control of branching and forking to maintain a dominant central stem. In my previous study, the two emergent types (*Liriodendron tulipifera* and *Liquidambar styraciflua*) showed the least tendency to lean, even when they were severely overtopped. Even intolerant, fast growing, bottomland species will not respond to sidelight when they are emergent types.

A final case that must be considered is trees growing in rocky habitats or grasslands. Such trees typically occur alone or in small clumps. Those growing at the edges of clumps are unlikely to be overtopped if they grow outward, and selection pressure will favour a phototropic stem response. My casual observation of prairie oak clusters shows significant tendencies to lean in these species.

In conclusion, an evolutionary logic determines which species will lean in response to asymmetric lighting. In general, species adapted to be canopy dominants will not respond to sidelight, but species that are small, short-lived, or from open habitats will. Small trees and shrubs will experience very little cost from leaning because of the natural elasticity of their wood. Large trees must be rigid and may pay a very high price.

This research is supported through contract W-31-109-ENG-38 by the US Department of Energy, Office of Energy Research, Office of Health and Environmental Research, and Program for Ecosystem Research.

REFERENCES

- Harper, J. L. & White, J. 1974 The demography of plants. *A. Rev. Ecol. Syst.* **5**, 419–463.
- Ishii, R. & Higashi, M. 1997 Tree coexistence on a slope: an adaptive significance of trunk inclination. *Proc. R. Soc. Lond. B* **264**, 133–410.
- Loehle, C. 1986 Phototropism of whole trees: effects of habitat and growth form. *Am. Midland Nat.* **116**, 190–196.
- Oliver, C. D. & Larson, B. C. 1996 *Forest stand dynamics*. NY: Wiley.
- Strauss, S. H. & Ledig, F. T. 1985 Seedling architecture and life history evolution in pines. *Am. Nat.* **125**, 702–715.

Received 20 May 1997; accepted 10 June 1997