















Brathay, Cumbria
18.4m high
144.5cm trunk diameter

Healthy, defect free trees appear to be designed to withstand most natural events that are foreseeable in their natural range.

- They have sufficient roots to supply water and mineral nutrients.
- They have sufficient photosynthesising area to provide carbohydrate for respiration, growth, defence and reproduction.
- They are mechanically strong enough to have a reasonable safety factor and withstand foreseeable windstorms and snow fall

HOW DO THEY DO THIS?



Outreach

Warnell School of Forestry & Natural Resources

UNIVERSITY OF GEORGIA

Tree Growth Regulation & Control Process

by Dr. Kim D. Coder, Professor of Tree Biology & Health Care, University of Georgia

NOTE: This publication is a synthesis of the tree growth regulation and correlation literature. General processes and systems presented here represent educational models which professionals can use to better appreciate and understand basic tree functions. These models do not represent actual physiological mechanisms, but simple theoretical means of explaining tree reactions within the environment.

A critical feature of tree growth regulation involves functionally balancing the top of the tree with the bottom. Concepts of shoot / root ratios and how a tree can maintain a resource balance between apparently competing needs have been proposed and tested for accuracy. Of all the working models examined, one form has proven over the last two decades to serve in simply describing regulatory partitioning between shoot and root in trees. This model is called a "Thornley" model, although many derivations and more refined systems exist.

The result of this model is to serve as a means for understanding tree functions in a holistic sense and predicting resource allocation patterns between shoot and root. Generically, shoot size and function is equated with root size and function. The purpose of a shoot is to utilize soil gathered resources to capture and ship carbon to a root. The purpose of a root is to utilize carbon to capture and ship soil resources to a shoot. Using only a few basic attributes of shoot and root can estimate the scale and intensity of shoot / root interactions. Figure 1

Estimating Balance

To calculate the proportional change patterns seen in trees, or their "functional balance," only four components are required under this model: sapwood shoot mass, sapwood root mass, photosynthesis rate, and nitrogen uptake rate. Figure 2 Trees will attempt to balance shoot mass and photosynthetic rates against root mass and nitrogen uptake. A tree will adjust the mass of roots or shoots to correct any deficiency in photosynthesis rates or nitrogen uptake. Carbohydrate shortages will initiate more shoots and nitrogen shortages will initiate more roots.

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- My colleagues past and present
- Ancient Tree Forum
- David Lonsdale
- Prof. Steve Woodward, Aberdeen University
- Ted Green
- Frank Rinn
- Claus Mattheck
- Karl Niklas
- Kozlowski and Pallardy x 2
- Ken James
- Lynn Boddy and co-workers
- Shigo – static (dead) and dynamic (live) biomass
- Neville Fay
- Jon Harthill
- David Evans
- And many others
- Arbcology wood decaying fungi for arborists and mycologists Facebook group

<https://www.warnell.uga.edu/sites/default/files/publications/WSFNR-17-04%20Coder.pdf>

The balancing tree

Trees strive to be balanced

- Mechanically (axiom of uniform stress – they have evolved to have a certain safety factor)
- Functionally:
 - Energetically: carbohydrate allocation for balanced growth of the different parts (roots, including mycorrhizal symbionts, sapwood, bark and leaves), maintenance respiration and defence;
 - Hydraulically: root activity, including the activity of associated mycorrhizal fungi, is in balance with the soil and the tree's moisture and mineral requirements.



The balancing tree

Trees, when healthy, have evolved to achieve those 'balances' – function and mechanical stability

These balances are achieved through a combination of the efficient use of available resources and an internal feedback system provided by plant growth hormones triggered by internal and external conditions.



The balancing tree

The 'balances' formed by a tree between its different parts will depend, to a certain extent, on its genetic makeup and the environmental factors it experiences: location and weather.



The balancing tree

For instance, a tree growing in a dry sandy soil will allocate resources to grow proportionately more roots per unit of foliage than its clone growing in a moist loam soil. The limiting growth factor: light, water or mineral nutrient(s); will promote the growth of the tree part that obtains that limiting factor from its environment.



Limiting factor

Liebig law of the minimum, often simply called **Liebig's law** or the **law of the minimum**, is a principle developed in agricultural science by Carl Sprengel (1828) and later popularized by Justus von Liebig. It states that growth is dictated not by total resources available, but by the scarcest resource (limiting factor). The law has also been applied to biological populations and ecosystem models for factors such as sunlight or mineral nutrients.

(Wikipedia)



So, for a unit of photosynthesis, biomass ratios of leaves to roots, for a species or even clone, alter depending on local climate and soil!

Its not biomass that's important – its functionality

Karl Niklas and co-workers

Carbon Allocation Hierarchy

(Generalities, there are likely to be overlaps)

(Q.F. Oliver and Larson, 1996)

1. Photosynthesis for maintenance respiration of live tissue.
Respiratory requirements increase as trees grow.
2. Production of fine roots (including mycorrhizae) and leaves.
3. Flower and seed production .
4. Terminal and lateral branch growth, and root extension. Reaction wood may take higher priority than height growth. Renewal of phloem may be of equal or higher priority.
5. If carbohydrate is still available after all these requirements have been met, it will be used for the growth of xylem – increase in diameter – and resistance to P & D

Internal communication – feedback and growth promoter (plant growth hormones - phytohormones)

- Shoots produce auxin which is transported through phloem or symplast, depending on author, to communicate shoot health to roots. Strongest growing shoots produce most auxin.
(Hey roots, we're doing great up here, loads of sunshine, give us as much water and mineral nutrients as you can and we will produce loads of carbohydrate 😊)
- Roots produce cytokinin which travels through xylem. Strong growing shoots attract more than weakly growing shoots.
(Hey shoots, we have access to loads of water and mineral nutrients. Give us loads of carbohydrate so we can grow, abstract them from the soil and provide them to you and the rest of the tree 😊)

Internal communication – feedback and growth promoter (plant growth hormones - phytohormones)

Plant growth hormones are also involved in xylem growth, growth of reaction wood, compensatory wood. Principally auxin and ethylene.

Cambial cells in areas periodically experiencing compression or tension will attract or synthesise plant growth hormones that stimulate cambial activity. With these, cambial cells attract or are stimulated to use carbohydrate to fuel the growth of additional sapwood to compensate for potential mechanical weaknesses



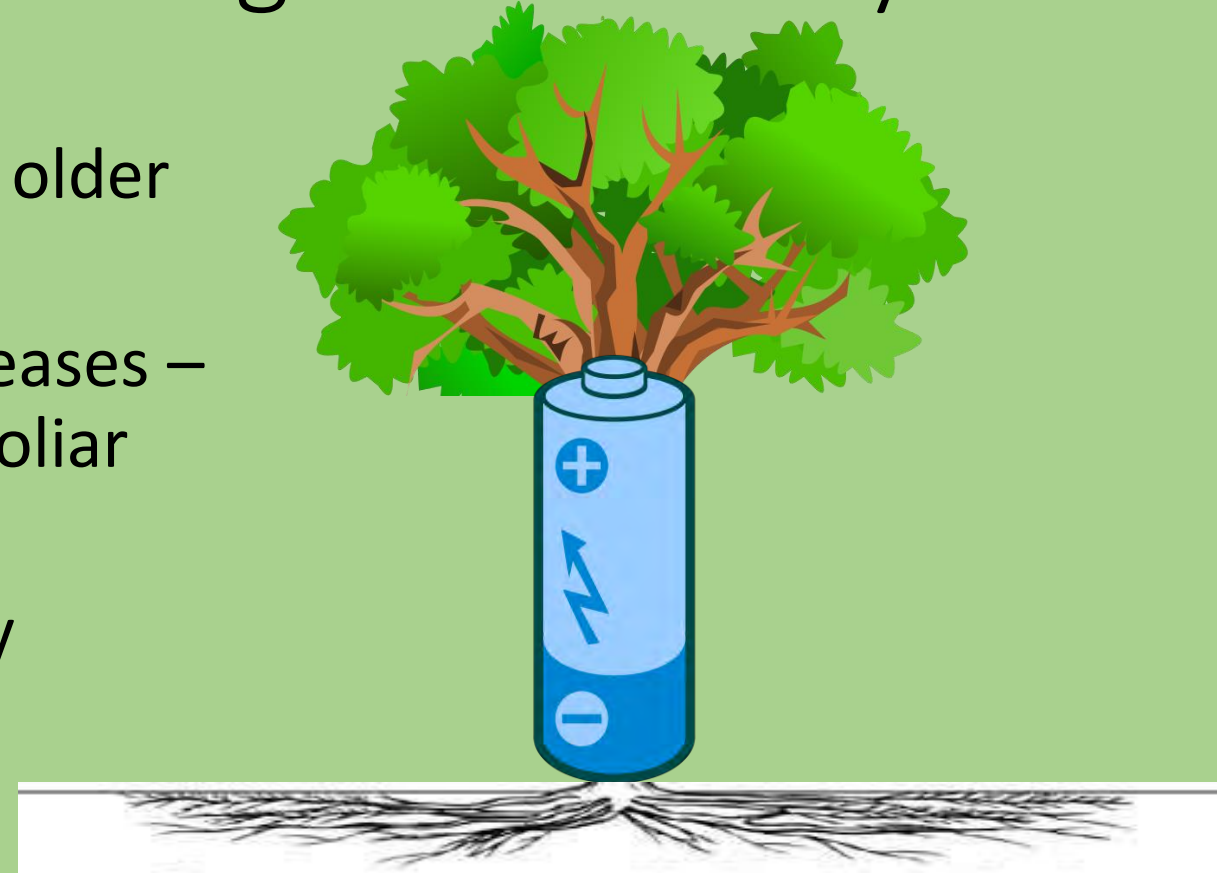
Sapwood for storage – rechargeable battery

- Stored non-structural carbohydrate (NSC) – energy – helps buffer trees against minor inclement events.
- Functional sapwood is therefore acting as a rechargeable battery.



Sapwood for storage – rechargeable battery

- One difference with a battery is that older parts die and new parts are grown.
- At times the size of the battery decreases – after drought, defoliation, pruning, foliar disease
- At other times the size of the battery increases – during periods when the weather is conducive for healthy growth and the crown expands



Sapwood storage

Damp North and West
Thicker band of live sapwood



Dry South East
Thinner band of live sapwood

Functional units (Lonsdale, 2013)

- A tree may contain a number of what have been referred to as ‘functional units’.
- A strong functional unit is part of a tree that is effectively self contained – roots, sapwood, bark, shoots and foliage.
- Some trees have strong functional units with little transfer of resources between one and another. Other trees, however, may not contain any functional units or only weak ones – the entire tree is one functional unit.
- A strong functional unit may occur when there is large branch, often fairly low down on a tree, which has direct xylem connectivity to specific roots. The branch supplies the roots with all their carbohydrate requirements and the roots supply the branch with all its water and mineral nutrient requirements.

Functional units (Lonsdale, 2013)

- In theory, if all the roots of a strong functional unit were to be severed and new ones were not allowed to grow, the sapwood and bark of that functional unit would die after all stored carbohydrate and water had been used.
- I suspect that the autonomy of a functional unit will decrease with increasing distance between branch and roots.



Latitude: 53.202407
Longitude: -1.069273
Elevation: 100.33m
Accuracy: 12.9m
Azimuth: 113° (SE)
Pitch: 3.4° (0.5°)
Time: 29-01-2019 10:59
Note: 8155

Old trees

Old trees often have short internodes and each node creates vascular friction – resistance – to sap-flow (Rust & Roloff, 2002). This has been observed to cause a reduction in photosynthesis in old oak trees (Rust & Roloff, 2002).



What happens if a tree becomes functionally unbalanced – **reduced crown activity?**

What happens when the photosynthetic ability of a tree is reduced, for instance by defoliating insects, leaf disease, late frost, or the removal of branches by pruning or storm damage?

- its requirement for water and nutrients is reduced
- its production of auxins and carbohydrate also reduces
- Initially there is an excess of roots and sapwood required to supply water and nutrients to the remaining crown
- The roots continue to produce cytokinin that, in turn, stimulates shoot growth in an attempt to re-balance the roots to sapwood to foliage ratio

What happens if a tree becomes functionally unbalanced – **reduced crown activity?**

- Initially the growth of replacement foliage reduces carbohydrate – energy – reserves
- If the tree experienced a significant crown reduction, the remaining foliage may not be able to produce sufficient carbohydrate to cover the respiratory requirements of all the live roots and trunk sapwood that existed prior to the crown reduction event.
- the remaining foliage requires a reduced amount of water and nutrients so some of the conducting sapwood and roots become excess to its requirements

What happens if a tree becomes functionally unbalanced – **reduced crown activity**?

- eventually, once excess tissue in roots and sapwood have respired all their stored carbohydrate they die (some stored carbohydrate may be transported to other tissue). Dead wood may be converted to ripe/heartwood but some may remain as dead sapwood.
- In time, if the tree doesn't die, it would re-balance – shoot growth would be stimulated and some roots and conducting sapwood would die – until it re-creates the hydraulic and energy production/use balance between its foliage, conducting sapwood and roots.



29/03/2019



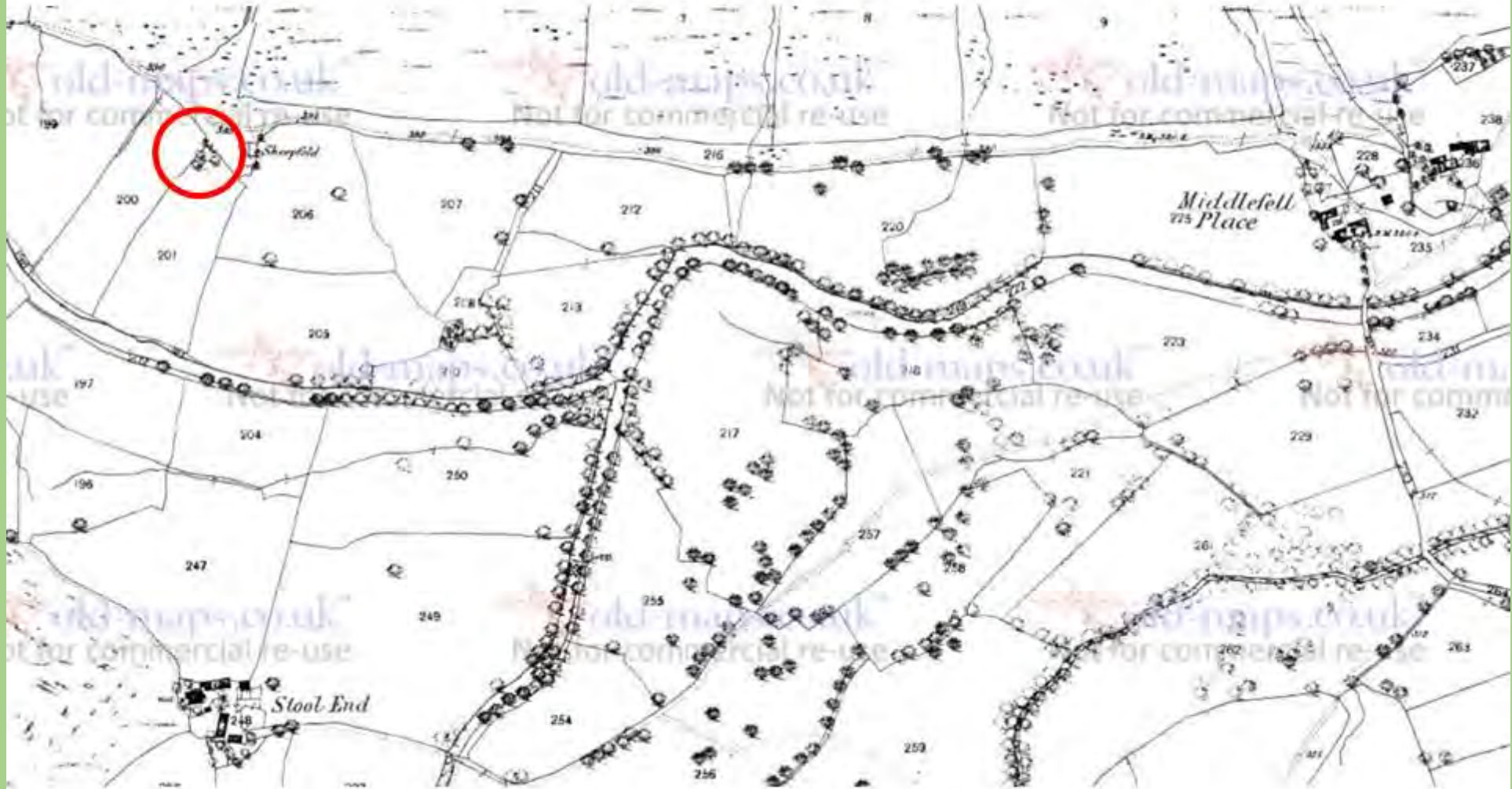
29/03/2019



23/03/2019

First Edition Ordnance Survey Map published in 1861

Scale 1:2500





23/03/2019



23/03/2019

What happens if a tree becomes functionally unbalanced – **reduced root activity?**

What happens when the ability of tree roots to obtain water and mineral nutrients is reduced?

- photosynthetic activity will also reduce
- reduced production of cytokinins which, in turn, reduces shoot and foliage growth
- initially, the foliage bearing shoots of the tree will continue to produce auxin which, in turn, stimulate root growth in an attempt to rebalance the different parts of the tree
- Eventually, if the tree doesn't die or blow over, it will become rebalanced through crown and sapwood death and additional root growth

Trees can tolerate 'normal' fluctuations of weather

Trees are 'programmed' – have evolved – to have a ratio of roots to sapwood to foliage that enables them to tolerate minor droughts and other foreseeable events. The actual genetic program of a particular tree will depend on its species and the conditions experienced by its ancestors. Trees growing in similar conditions to where their ancestors evolved will therefore tolerate, during most years, the loss of a certain amount of root activity due to 'expected' drought.

Stored non-structural carbohydrate (NSC) helps buffer trees against events which reduce photosynthesis/water and nutrient availability

Climate Change?

Extreme events leading to bark death

- Sapwood usually dies from the inside out – ripe/heartwood formation. However, if a tree loses a significant proportion of its crown or roots, sapwood death may cause entire strips of sapwood and bark to die that were serviced by the lost roots or foliage.
- Internal sapwood that becomes excess to a tree's requirements, in the UK, is usually converted into ripewood or heartwood but after extreme events some may remain as dead sapwood. Heartwood and ripewood don't contain living cells once fully formed. Some commentators suggest that live radial parenchyma may extend into heart/riewood. If so I suspect these cells are becoming increasingly moribund and less important for the tree.

Pollarding/Topping

- Some of the root systems dies and becomes available for decay fungi as does much of their internal branch and trunk sapwood
- A barrier zone, Wall 4 in Shigo's CODIT model, is formed during the first growth period after the tree is pollarded or topped
- Over time, the wood internal to the barrier zone will become colonised by decay fungi – eventually the trunk becomes hollow
- At the same time the tree grows new foliage bearing twigs that fuel the growth of new sapwood and roots

Pollarding/Topping

- Eventually, the tree will become physiologically rebalanced
- If not re-pollarded, the crown of the tree will continue to grow larger and be able to provide increasing amounts of carbohydrate for the maintenance respiration of increasing volumes of physiologically functioning cells, including in the cylinder of live sapwood outside the barrier zone. The cylinder of live sapwood increases in depth.
- In theory, once 'balanced', a healthy pollarded tree will continue to grow sufficient additional tissues to maintain the mechanical stability of all parts (Axiom of uniform stress).

Pollarding/Topping

- Eventually, as with trees that haven't been pollarded, a stage will be reached when the crown of the tree won't be able to synthesise sufficient carbohydrate for continued growth, reproduction and defence as well as maintenance respiration of all its sapwood.
- At this time some of the older internal sapwood won't be required and the tree will cease to provide it with carbohydrate. Consequently it will die and be converted to either heartwood or ripewood.
- Heart/riewood is available for wood decay fungi but commencement of decay may not proceed for some time.







Pruning trees to improve their health!

- Some people have suggested that that pruning trees with reduced vitality may improve the health of retained shoots.
- If the pruning significantly reduces the length of xylem between the roots and retained foliage, it will require less carbohydrate for maintenance respiration.
- The roots will continue to synthesise cytokinin which will stimulate shoot growth.
- Also, whereas the roots and sapwood may have been struggling to supply the foliage with its water and nutrient requirements, they can easily do so after the amount of foliage has been reduced.

Pruning tree to improve their health!

- It has been suggested by some commentators that the total increase of biomass produced each year after a tree has been pruned is less than it would have been if it had not been pruned.
- I suggest that further research on this is required.
- The Rusland Beeches are a line of veteran beech trees in Cumbria that are next to a road. In the past thirty years some have been pruned drastically to prevent catastrophic failure endangering road users. The health of these trees is now good with long twig extension and healthy looking leaves. However, decay is rapidly developing in the stems, roots and butts!

Ability to grow new shoots

- Some trees, either individuals or species, possess the genetic ability to grow foliage bearing branches from dormant or adventitious buds, whereas others don't.
- The majority of the mature beech trees in the UK don't appear to be able to quickly form new shoots after storm damage or pruning.
- However, there are some beech trees that have lots of epicormic shoots and could presumably form new branches after crown loss.
- Prof Julian Evans suggested that the ability of oak trees to grow epicormic shoots is partly dependant on their individual genome.

Is a tree healthy enough to be pruned?

- The energy status of a tree when it is pruned will determine whether or not dormant and adventitious buds will be able to grow into new shoots while maintaining sufficient live sapwood, roots and bark.
- Trees with low vitality that lose some or all of their foliage bearing branches may not contain sufficient stored carbohydrate to fuel shoot growth from dormant and adventitious buds.
- However, if the pruning operation is delayed, after a number of years of weather conditions suitable for healthy tree growth, and no other stressing factors, such as diseases and pests, the same tree may have adequate energy reserves and be able to readily grow new shoots.

Post branch loss weather conditions

Crystal ball gazing

- Weather conditions after foliage or root loss can affect a tree's ability to form new shoots/roots.
- If the weather conditions are stressful for tree growth they will reduce its ability to grow viable foliage/roots, and therefore also its long-term viability.



Standard guidance on pruning

- Reduction cuts less than 10cm diameter to a side shoot that is at least a third the diameter of the part removed.
- If we accept that there is a direct coloration between leaf area and cross sectional area of sapwood (pipe theory – modified by recent research).
 - 9cm diameter cut back to a 3cm diameter side shoot.
 - 9cm diameter – 63.62cm^2
 - 3cm diameter – 7.07cm^2
 - Summed area – 70.69cm^2
 - Percentage retained – 10%
 - Percentage lost 90%!!!
 - At time of pruning that is a reduction in leaf area – photosynthetic function – of 90%!!!

Factors to consider before pruning an ancient or valuable tree

- Likelihood of failure.
- Failure point.
- Tree health.
- The ability of the tree to increase its foliage area after the work has been carried out.
- The proportion of the tree's foliage bearing branches and twigs will be retained and their effect on the mechanical stresses applied to the predicted failure point.
- The habitat value of the tree, both before and after the work is carried out compared to its habitat value if it were allowed to fail.

Factors to consider before pruning a tree

Pruning may increase mechanical stability but reduce biological viability

It is a compromise!

When to work on ancient trees

- I suggest that **no work** should be carried out to trees assessed to be stable.
- I suggest that **work should** be carried out to a tree if it **will prevent** catastrophic failure of a significant part of its crown and **will prolong** the life of the retained crown and associated sapwood and roots, and the duration of habitat provision.
- I suggest that **no work** should be carried out to a tree with low vitality **unless** it is accepted that it may kill it but **will** preserve standing dead wood habitat as an alternative to allowing it to fail catastrophically.

When to work on ancient and valuable trees

- I suggest that **no work** should be carried out to a tree with a large crown that is only at risk of losing a small proportion of its foliage bearing branches.
- I suggest that **work should** be carried out to a tree if it **will prevent** catastrophic failure that is likely to kill it and the work **will prolong** its life, the duration of the habitat it contains and its ability to grow new sapwood.
- I suggest that work **should only** be carried out to a dead tree where it is judged there is an imminent risk of failure and where the work will enable it to stand for longer and continue to provide standing dead wood habitat.

Summer Branch Drop – proves or disproves axiom of uniform stress!

Characteristics

- Long, poorly tapered lower branches
- Foliage concentrated at the distal end – striving for light
- Higher branches shade all but the distal end of the branch
- Branch fails leaving a stub that is 3-7 times longer than its diameter

Do you remember this next slide?

Carbon Allocation Hierarchy

(Generalities, there are likely to be overlaps)

(Q.F. Oliver and Larson, 1996)

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Summer Branch Drop – proves or disproves axiom of uniform stress!

Hypothesis

- Most of the length of the branch is shaded – leaves only at the distal end
- The branch has high maintenance respiratory requirements but a relatively small photosynthesising area
- The branch allocates carbohydrate to extend out of the canopy to obtain light at the expense of increasing in girth
- Branch taper reduces
- Branch breaks once the taper is so low that it is not able to support the branch
- The final factors that lead to branch failure may include breakage of water columns in xylem or lignin and pectin becoming plastic due to heat

Conclusions

- At times it is beneficial to prune trees.
- We need to be aware of changes that will occur within a tree after it has been pruned.
- Trees often contain dysfunctional wood and, if it is protected from drying out by a complete sheath of live bark and sapwood, it does not decay or decays very slowly.
- After pruning the biggest change will be a reduction in depth of live sapwood – **this is out of sight!**
- Biological changes will be insignificant if only a small amount of foliage bearing crown is removed
- Removing a small amount of crown will reduce risk of mechanical failure by a small amount and regrowth will, in time, eliminate this benefit.

Conclusions

- Pruning by a small amount will have a small impact on a tree's biological viability and improve its safety factor by a small amount.
- Pruning by a large amount will have a large impact on a tree's biological viability but improve its safety factor by a large amount – the tree may survive but with much less live biomass.
- How much to prune can be a compromise between biological viability – amount of live biomass – and mechanical stability

Thank you

Is there time for questions?