What Does Science Say About Pruning Mature Trees?

I. Introduction
  A. Definitions
    1. Aging - environmentally induced
      a) Decrease in performance
      b) "Mere passing of chronological time"
    2. Senescence - genetically programmed
      a) Mutations
      b) Molecular changes
    3. Which is more valid for ancient trees? (definitely not genetic)
      a) Example: bristlecone pine
      b) No mutational increases with age (high altitude trees)
      c) Decline in growth is reversible (thinning, other ways to decrease competition or increase resources - water most likely)
      d) Therefore genetic senescence does not happen
  B. History of Research on Older Trees
    1. Production forestry
      a) Timber stand management
      b) Removal of lower branches to decrease knots
      c) Interest in process of self-pruning
    2. Fruit, nut, and wood production
      a) Coppicing and pollarding
      b) Maintaining low crowns
      c) Removal of older limbs to short stubs; no scaffold limbs helps increase density (tall spindle production)
  C. Literature reviewed
    1. Peer-reviewed, scientific articles
    2. Papers published within the last 20 years

II. General Tree Morphology and Physiology
  A. Reiteration of units
    1. Immediate - apical buds
    2. Delayed - epicormic buds
    3. Adaptive reiteration
      a) Occurs outside of trauma - different than epicormics release
      b) Increases branch longevity - "bud bank"

c) *May prolong tree longevity*

d) *Lower growth rate may be adaptation for old trees to optimize resource use efficiency*

B. Modeling

1. Architectural - reiteration of units
2. Physiological - reiteration, but pruning changes response

C. Sapwood dynamics

1. Outer sapwood connects surface roots to sun leaves
   a) *Decrease in water leads to a decrease in sun foliage*
   b) *Decrease in photosynthesis leads to a decrease in transportation to roots*
2. Can be low in outermost due to underdeveloped outer xylem (newest)
3. Can be low in innermost due to loss of functional inner xylem by blockage

D. Comparative physiology

1. Outer and mid-canopy leaves are main sink for N during vegetative growth; become source during reproductive growth

III. Physiology of Aging Trees

A. Ancient trees

1. Extraordinary long lived
2. Often harsh environments - no pests or disease
3. Very little known about their physiology and many assumptions incorrect
   a) *Can't rejuvenate, because it's not genetic aging (senescence)*
4. Do not appear to senesce

B. Why does growth decline?

1. Not senescence/genetics
   a) *Parts may die, but organism does not*
   b) *Size, not age, drives development changes*
   c) *Grafting young tissue on old branches or old tissue on young branches - takes on characteristic of rootstock*
   d) *"rejuvenation" is inaccurate terminology, since that implies senescence*
2. Hydraulic limitation hypothesis
   a) *Gravity*
   b) *Longer pathway*

c) *More tortuous pathway*

d) *Decreased allocation to roots*

3. Crown reduction may be a temporary form of adaptation to insufficient water

4. Decrease in soil nutrients

5. Other environmental factors can influence

a) *Sudden water availability*

b) *CO_2 increases with climate change*

(1) Could increase maximal height

(2) More CO_2, less photorespiration

C. Changes with maximal height reached

1. Girth continues to expand

a) *Increased mechanical support*

b) *New vascular tissue*

2. Tops often flattened with chronic dieback

3. Stems and foliage of older trees

a) *More nodes*

b) *Shorter, thicker stems and smaller, thicker leaves than young*

c) *Increased longevity*

d) *Decreased photosynthesis*

e) *Increased WUE*

f) *Xeromorphic foliage (i.e. water stressed) character*

(1) Less mesophyll

(2) Increase in astrosclerids - structural defense

(3) Increased chemical defense - tannins

(4) Increased antioxidants

g) *Will revert to primary foliage under stress (e.g. pruning)*

4. Cladoptosis increases with increasing age, decreasing vigor

5. Can be reversed if competitors removed; increased water availability

D. Lower branch contributions

1. Feed trunks and roots

2. Are less productive than higher in the crown

IV. General Effects of Pruning on Trees - all relevant to ancient trees

A. Need to understand how live crown removal affects growth

1. Pruning dwarfs trees

a) *The greater the crown removal, the greater the reduction in ring growth and canopy years later*

b) *Summer pruning decreases carbon fixation proportionally*

c) *Renovation pruning increases fruit and nut production at the expense of girth*

2. Thinning cuts have little effect on bud growth
3. Heading cuts stimulate bud growth

B. Severity of wound and vigor of host influence response and survival
1. Epicormic shoots most likely when crown reduction 40% or more
2. Emerald ash borer most likely to lay eggs on trees with 40-60% of crown removed

C. Biggest impact on roots and lower stem
1. Change in carbon allocation to secondary axes
2. Secondary axes become a significant sink - no photosynthetic output
3. Reduces taper as well as girth
4. Creates deficit for roots
   a) *Growth*
   b) *Nitrogen-fixing bacteria*
   c) *Mycorrhizal fungi*

D. Severely pruned trees most likely to die indirectly
1. Older trees are less likely to recover from pruning than younger trees (compensatory response)
2. Stressed trees attract pest insects (e.g. pine beetles)
3. New growth attracts browsers
4. Large branch pruning has increased associated costs
   a) *take longer to seal*
   b) *increase the chance of pathogen entrance*
      (1) Nectria canker with winter pruning

V. Pruning Aging Trees - Natural and Artificial Methods

A. Wound response
1. Severity
2. Tree vigor
3. Decreased nitrogen levels as pool is housed in outer canopy leaves

B. Self-pruning (cladoptosis)
1. Clad = stem; ptosis = falling
2. Creates abscission zone

a) *On average, branches died 7 years after their growth cessation*

b) *Breakage different between young and old branches: older requires mechanical force*

3. Species specific - some do, some don't

4. Cladoptosis is determined by physiological conditions triggered by environmental factors

a) *Decrease in light*

(1) ↓ in photosynthesis → ↓in sapwood flux

(2) ↓ in transpiration → ↓ in inner xylem flow

(3) Inherent shade tolerance and self-pruning behavior supports a carbon based mechanism for branch mortality - mediated by an asymmetry in light exposure of the crown. But these are all stand dynamics - may be different for individual trees

b) *Decrease in available water*

c) *Fire survival/avoidance*

(1) Characterized by thick bark, height, and self-pruning of dead branches.

(2) Trees that retain dead branches are more likely to carry a fire into the canopy than a tree that self-prunes.

C. Crown removal

1. Concerns

a) *Dead wood is a source of pathogen spores*

b) *Damage from increased exposure of shade leaves to full sun*

2. Topping

a) *Decay - increases dead stubs*

b) *Structural integrity decreased*

c) *Aesthetically unappealing*

3. Crown reduction

a) *Cuts back to a live lateral*

4. Pollarding and coppicing

a) *Branches are young (3 years old or younger)*

(1) Usually callus over

(2) Disease compartmentalized

(3) Properly done, process can increase life span of trees

b) *Increases biodiversity with increased structural complexity*

c) *Decreases carbohydrate reserves*

d) *Does not rejuvenate, since it does not change genetic programming*

e) *Requires yearly maintenance*

f) *Overmature pollards are difficult to restore and are prone to crown collapse*

5. Rejuvenation

6. Retrenchment often attempted to reduce the risk of the tree splitting apart and to promote growth of new branches from the lower part of the tree

VI. Recommendations

1. Ancient trees cannot be "rejuvenated"
   a) *Cannot be coppiced or pollarded*
2. Avoid unnecessary opening of canopy
   a) *Sunburn of bark*
   b) *Increase photoinhibition of inner canopy leaves*
3. Do not leave-stubs
   a) *Hazardous to tree workers*
   b) *Increase epicormics bud release*
      (1) Leads to increased shading
      (2) Leads to canopy congestion

For more information

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