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WHOLE TREE INTERACTIONS

Advanced Tree Biology

(Part 3 OF 3)

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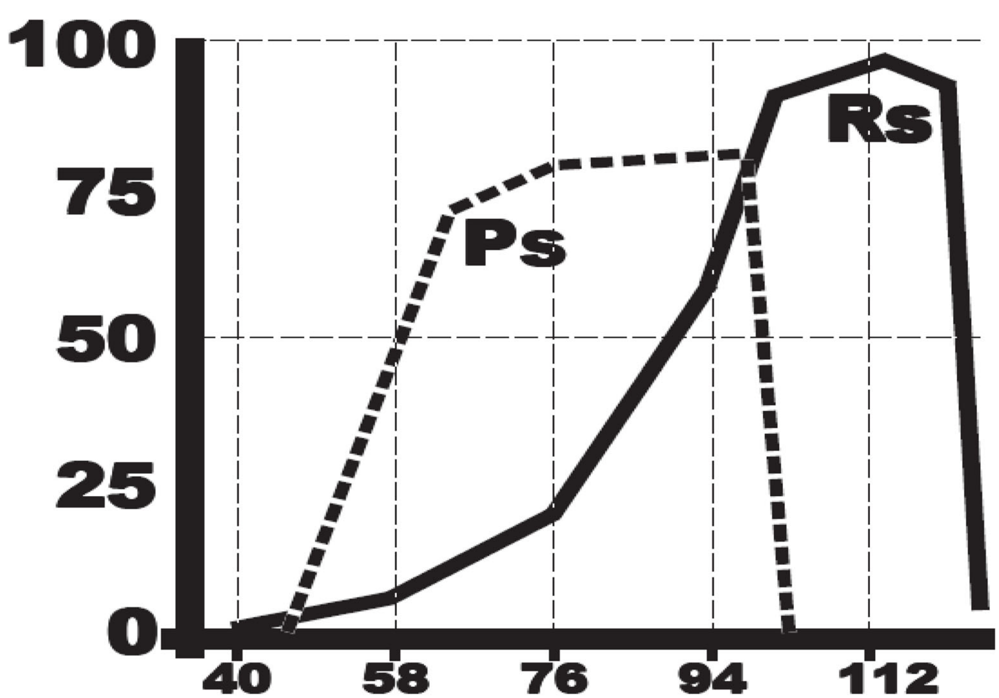

Scope & Disclaimer: This is part 3 of a three part training manual designed for helping advanced tree health care providers and senior community foresters appreciate and understand basic tree physiology -- specifically whole tree interactions of photosynthesis and respiration. This educational product is a synthesis and integration of current research and educational concepts regarding processes allowing trees to survive and thrive. This educational product is for awareness building and professional development at an advanced level. This product does not present detailed tree physiology in depth, nor with complete coverage of the subject. This training manual represents a simple, although strenuous, review drawn from key books and research papers on plant and tree biochemistry, functional physiology, and environmental interactions. This manual is meant as a knowledge foundation guide for understanding tree life.

At the time this third revision was finished, this training manual contained educational models concerning tree physiology thought by the author to provide the best means for considering fundamental tree health care issues surrounding whole tree interactions of photosynthesis and respiration. The University of Georgia, the Warnell School of Forestry & Natural Resources, and the author are not responsible for any errors, omissions, misinterpretations, or misapplications from this educational product. The author assumed professional users would have a basic tree biology background. This product was not designed, nor is suited, for non-tree professionals or homeowner use. Always seek the advice and assistance of professional tree health care providers.

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Whole Tree Interactions:

Advanced Tree Biology (Part 3 of 3)

Tree growth and health are the product of an environmental equation starting with photosynthetic productivity. The components of tree growth include the timing of when photosynthesis occurs in the year, the amount of photosynthesis generated compared to the amount of respiration, how photosynthate is divided among parts and different states within a tree, and how many leaves are produced. All of these combine with whole tree photosynthetic rates to yield a final solution of how well a tree grows and maintains health.

Photosynthetic rate and capacity is best estimated over several years as the amount of dry weight accumulated (i.e. net C captured). There are many other measures used in trees (some from herbaceous plant research), many of which are made over short durations and do not necessarily integrate all environmental constraints. For example, photosynthesis per leaf, leaf area, leaf weight, and amount of leaf chlorophyll have all been used to suggest photosynthesis effectiveness. These measures are a single snap-shot in time. Long term (multi-season) measures are best for trees.

Ps Differences

There is an inherent difference in photosynthesis between angiosperms and gymnosperms. Many angiosperms are roughly as efficient in photosynthesis at low light intensities as at high light intensities. Most gymnosperms are most efficient at high light intensities. Because many gymnosperms and some angiosperms are evergreen (seasonally non-deciduous), they may generate as much or more total carbon fixed than higher efficient deciduous species due to a longer growing season. Evergreen gymnosperms may generate >60% of their photosynthate on either side of a traditional growing season.

Gymnosperms gradually increase photosynthesis in Spring over a two to three month period as climatic resources change. Photosynthesis then gradually declines in Fall. Frosts, cold soils, and cool day temperatures are controlling factors. Photosynthesis in Winter is measurable if soil water and non-freezing temperatures are present. During Winter warm-up or thaws, significant photosynthesis can occur in evergreen gymnosperms. As freezing temperatures reach below 24^{o}F (-4^{o}C) for short durations, photosynthesis is inhibited for longer periods of time. Figure 1 shows photosynthesis per tree gradually increases and decreases across the seasons in the North American temperate zone.

In deciduous angiosperms, photosynthesis rapidly increases in Spring as leaves expand and rapidly decreases in Fall as leaves senescence. Ring porous vascular architecture trees tend to reach peak photosynthesis by early Summer while diffuse porous trees tend to add leaves over Summer and maintain them into Fall. The ability to sustain functional leaves and strong photosynthesis into Fall for diffuse porus trees allows for relatively rapid growth, although at some risk of resource loss from adverse weather.

Leaf Life

Throughout the crown of a tree, each leaf has a different light environment to which to adjust. Different photosynthesis rates are found in each leaf. Leaves in shade (33% - 66% full sun) are structurally designed to effectively utilize shade resources. Leaves in full sun (90% -100% full sun) are structurally designed for sun resources. Leaves developed in highly shaded conditions (10% - 33%), are marginal producers and are usually targeted for senescence. Figure 2.

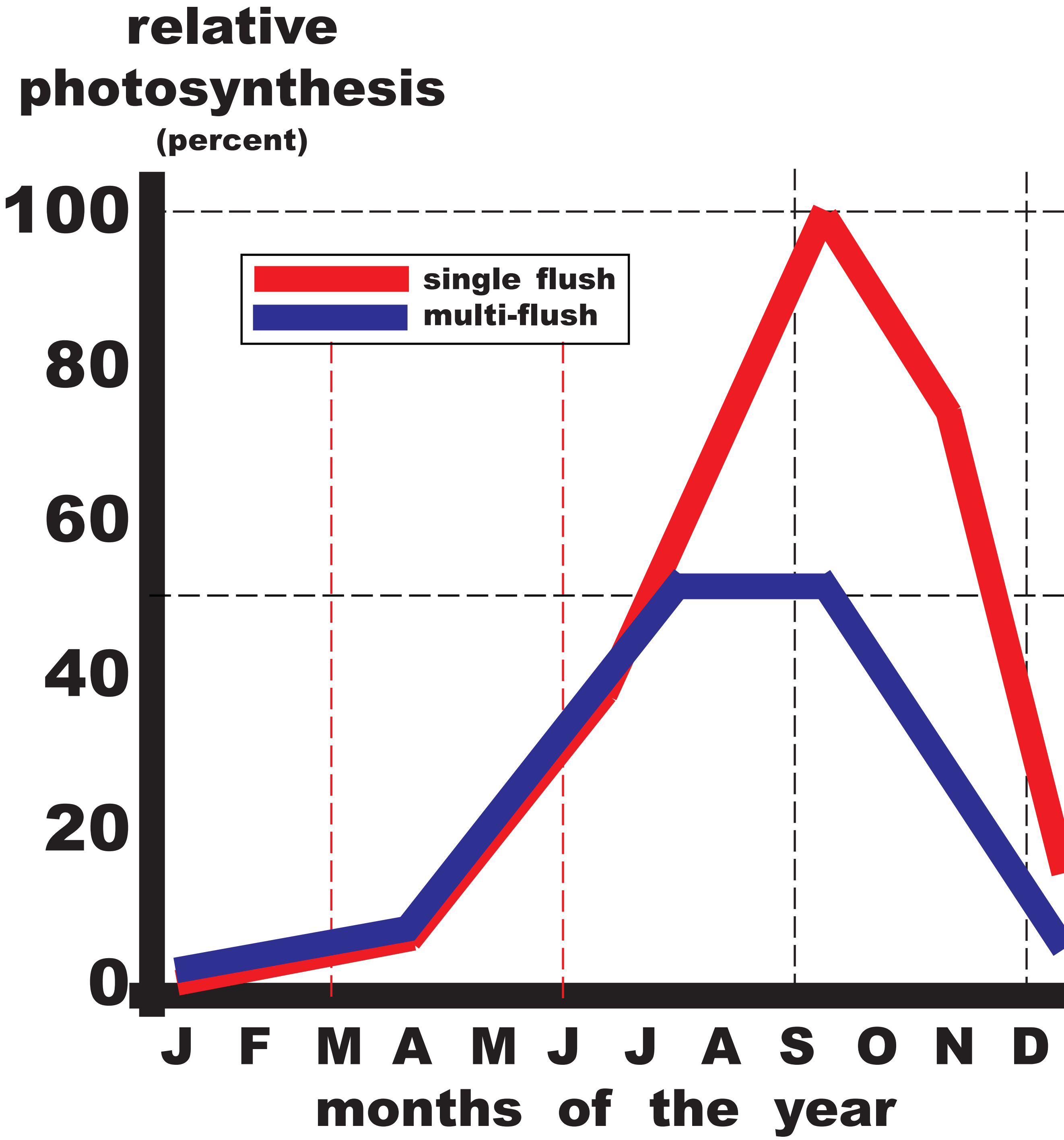

Figure 1: Evergreen tree photosynthesis over a year for a multi-flushing and a single flush species.
(modified from Pallardy 2008)

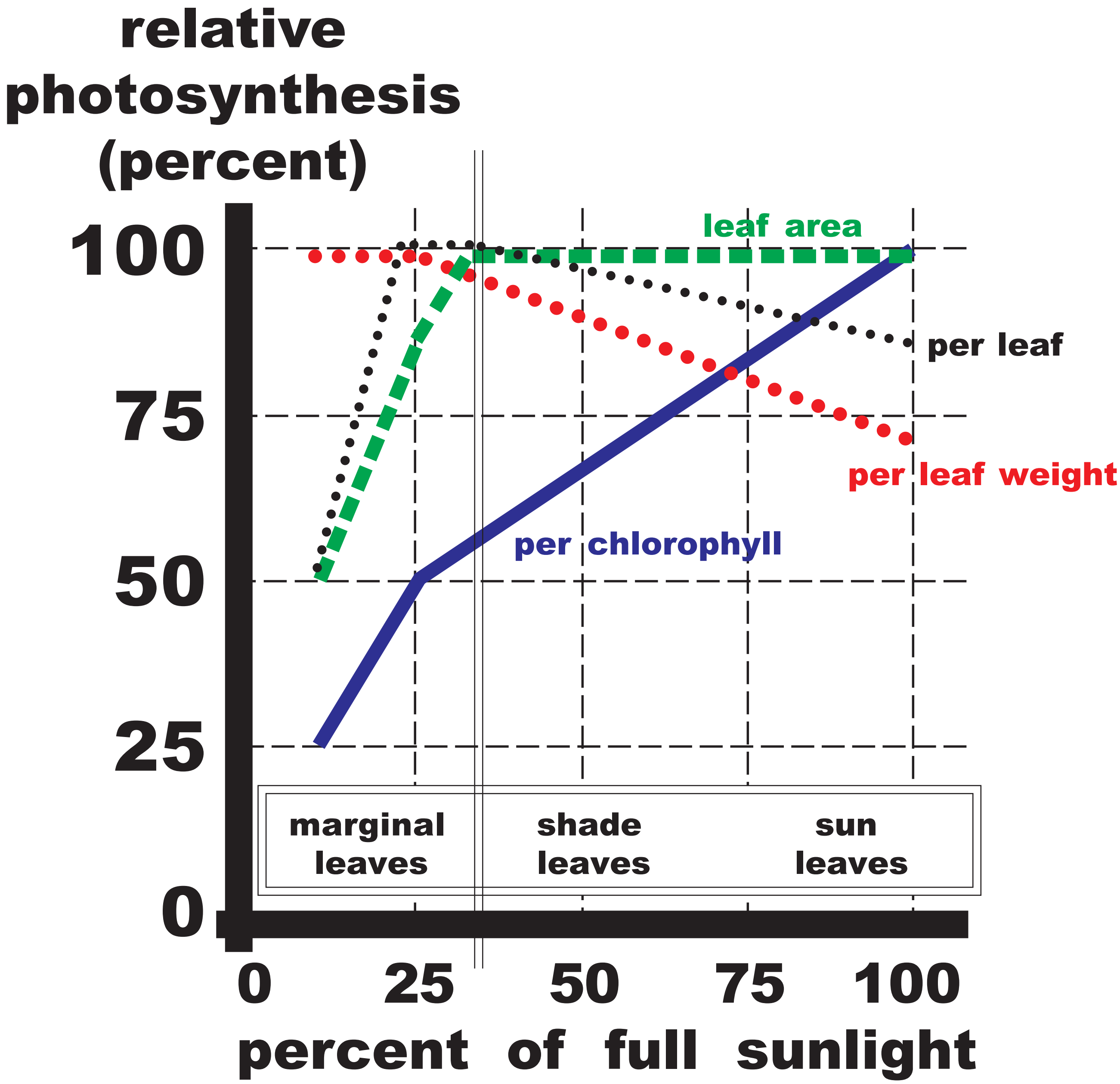

Figure 2: Photosynthesis in leaves per leaf area, per leaf, per chlorophyll, and per leaf weight. The line at 33% of full sunlight represents a boundary between efficient shade leaves and marginal leaves. Below 10% of full sunlight is leaf death. (from Flore & Lakso 1989)

As usable light striking a leaf increases in intensity, key indices of photosynthesis increase and then level out. A leaf reaches light saturation where photosynthesis machinery is operating at peak levels. As more light intensity is added, photosynthesis can not increase because it is already operating at its maximum. This is seen in two components -- leaf area and leaf nitrogen levels where both approach maximum levels between 65-85% full sunlight intensity. Figure 3. Additionally, because of self shading and resource limitations in different parts of the crown, increasing light intensity does not continue to increase productivity.

Day Tripping

The daily change in photosynthesis is closely tied to light intensity from sunrise to sunset. Trees in shade of other trees have photosynthesis rates associated with the number and duration of sunflecks, and average shaded light intensity. Many temperate trees have two photosynthesis productivity peaks each day, with a mid-day decline caused by high light intensity and/or water deficit peaks. Figure 4.

Figure 5 shows a relative mid-day reduction of photosynthesis on both cloudy and sunny days, with high light intensities limiting photosynthesis significantly. On cloudy days, trees are more effective in gathering and using sunlight. Sunny days mean more leaves are operating above light saturation, essentially wasting light and damaging photosynthetic machinery.

Stressed In

If water shortage from excessive stomatal transpiration occurs, stomates close and high light intensity continues to cause chlorophylls to fire, creating photosynthesis inhibition problems and damage. Carbon loss cycle (photorespiration) increases with light intensities and produces CO2 which is then partially reused by photosynthesis but with a significant energy loss. More light with limited atmospheric CO2 also increases the xanthophyll cycle and shifts more energy into heat.

Figure 6 shows how light energy in a tree is distributed during the day to various uses. The decrease in pH from high light intensities changes the LHCII proteins and shifts their positions to minimize damage or wasteful energy pathways. Usually by the next morning photoinhibition caused during mid-day the day before is almost gone.

Photosynthesis is impacted by the environment through the level of stomate opening, leaf area, and leaf cell capacity for CO2 absorption and light capture. Abiotic impacts can include light intensity, temperature, water, and element availability, all of which can cause photoinhibition when away from optimal values. Too much or too little essential resource messes things up! For example, Figure 7 shows the impact of water / drought on photosynthesis. The negative aspects of abiotic stress can be somewhat mitigated by careful tree health management (i.e. arboritecture, tree placement, advected heat shielding, irrigation, fertilizer, etc.).

Light Comp

As light on a tree increases from complete darkness where no photosynthesis is occurring to full sunlight, two points are reached which define photosynthesis for any tree. In the dark, living leaf cells respire and generate CO2. As light intensity increases, more and more internal CO2 is used in increasing photosynthesis until the amount of CO2 respired (released) by leaf cells is equal to the amount captured by quickening photosynthesis. This point where internal CO2 produced and CO2 used in photosynthesis is equal is called the light compensation point. Figure 8.

For example, shade leaves will reach light compensation point at lower light intensities than sun leaves. Sun leaves have a tremendous maintenance respiration load (i.e. produces a lot of CO2) to over-

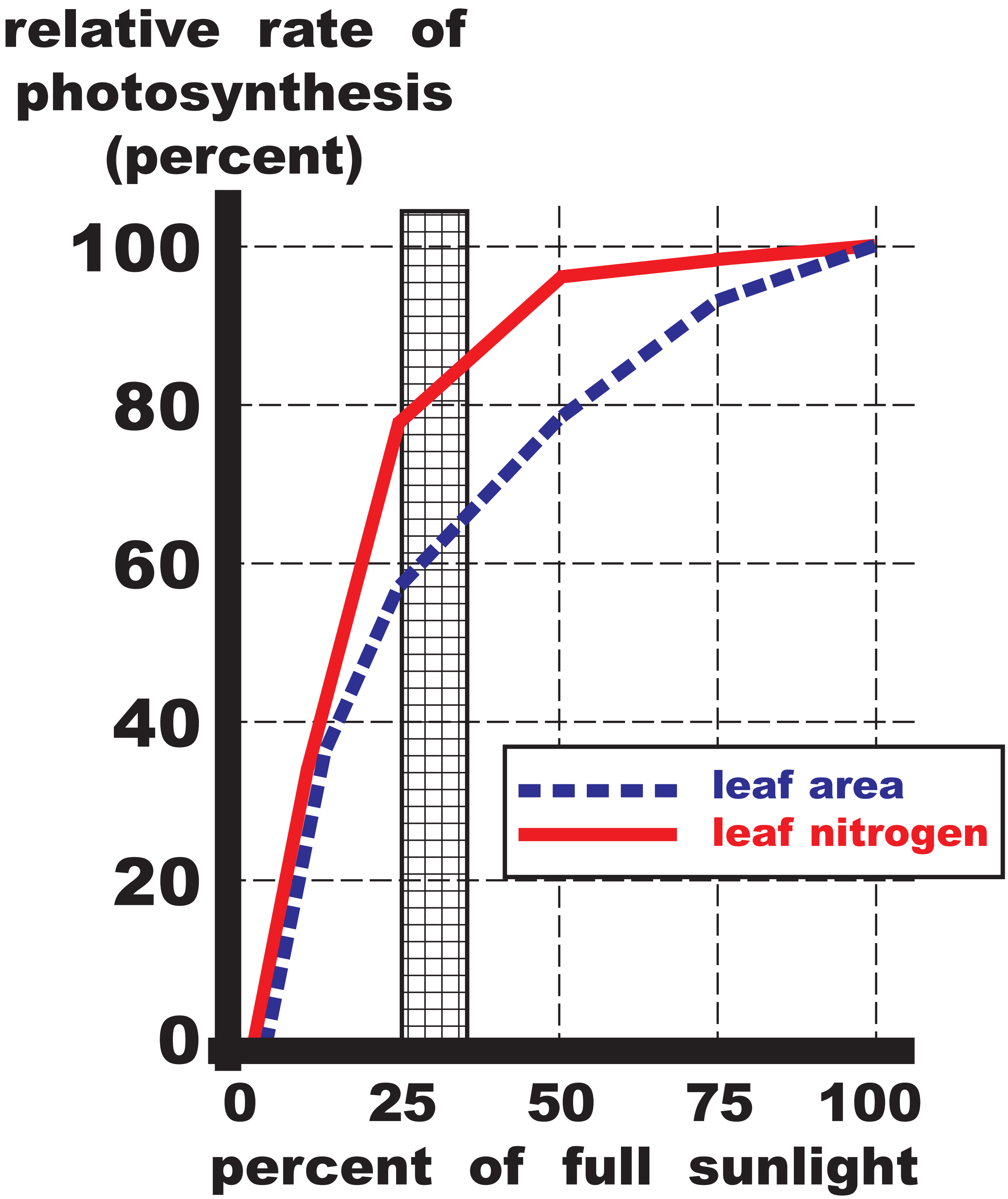

Figure 3: Relative light intensity impacts on tree photosynthesis based upon leaf area and leaf nitrogen content. Shaded box is dividing line between shade and marginal leaves.
(derived from DeJong 1986)

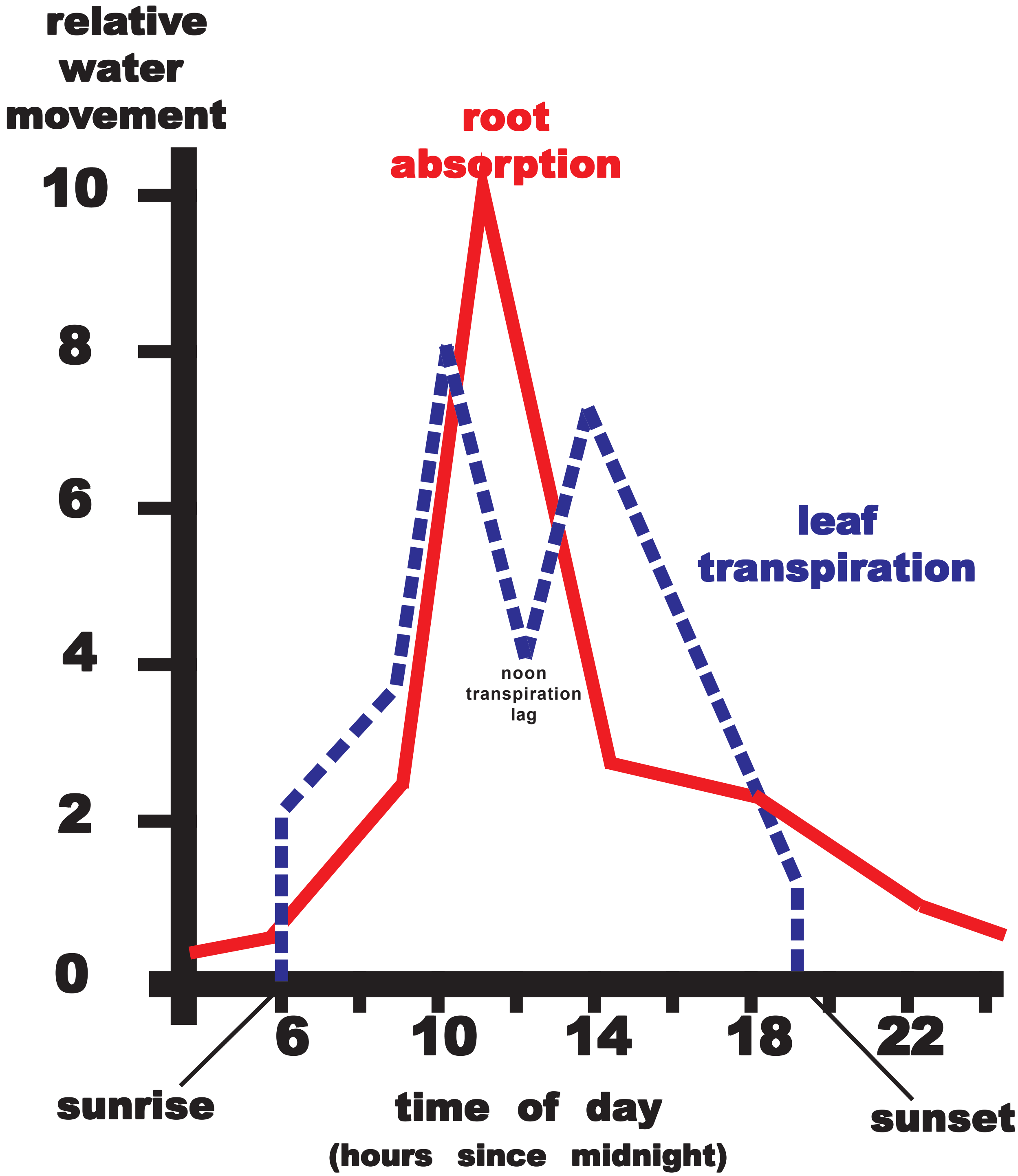

Figure 4: Root absorption and leaf transpiration within a tree. Note transpiration in leaves begins just after sunrise, is slowed at mid-day, and stops just before sunset. Root absorption continues through the night.

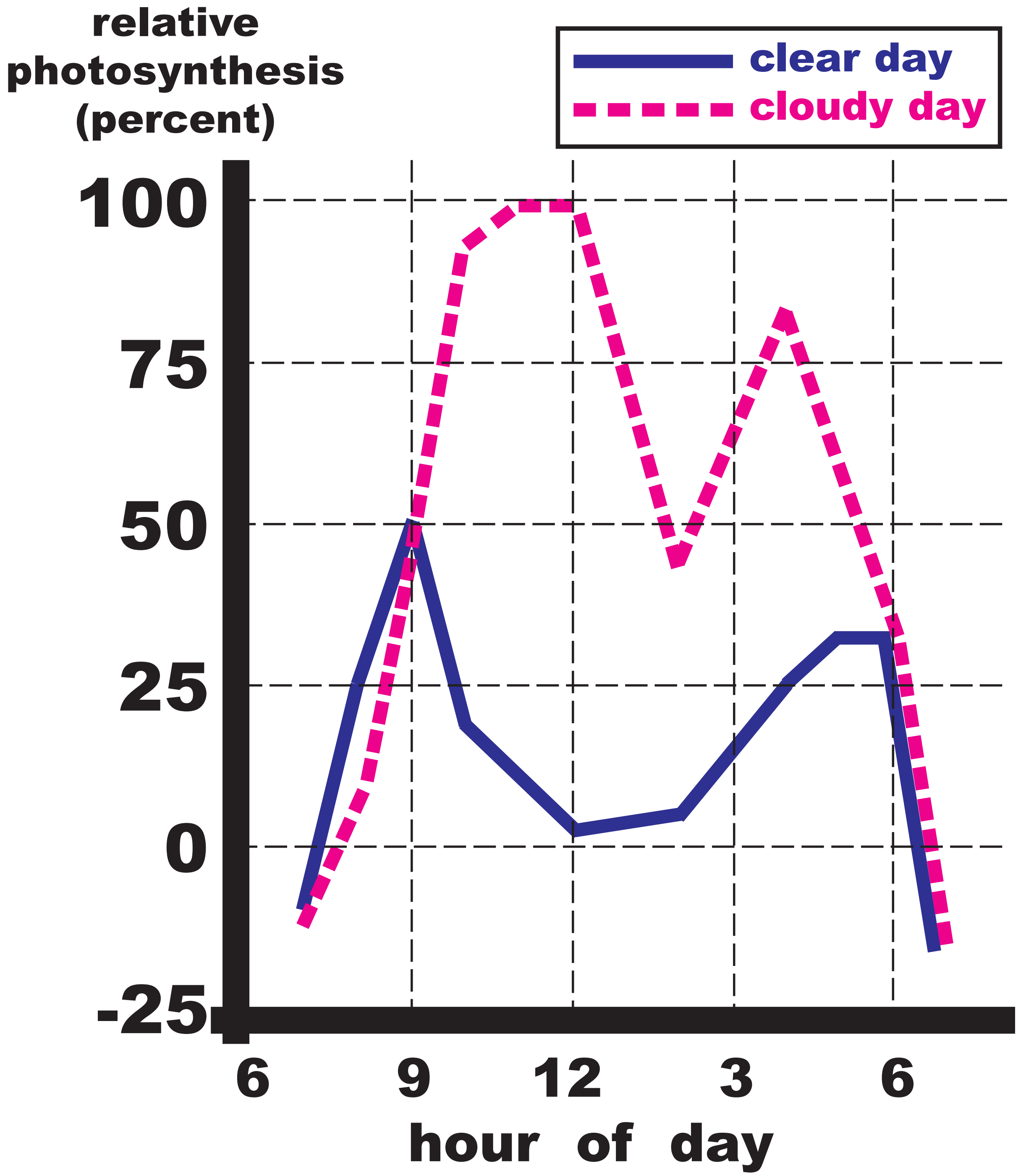

Figure 5: Impact of a growing season daytime cloud cover on relative tree photosynthesis.
(from Pereira et.al. 1986)

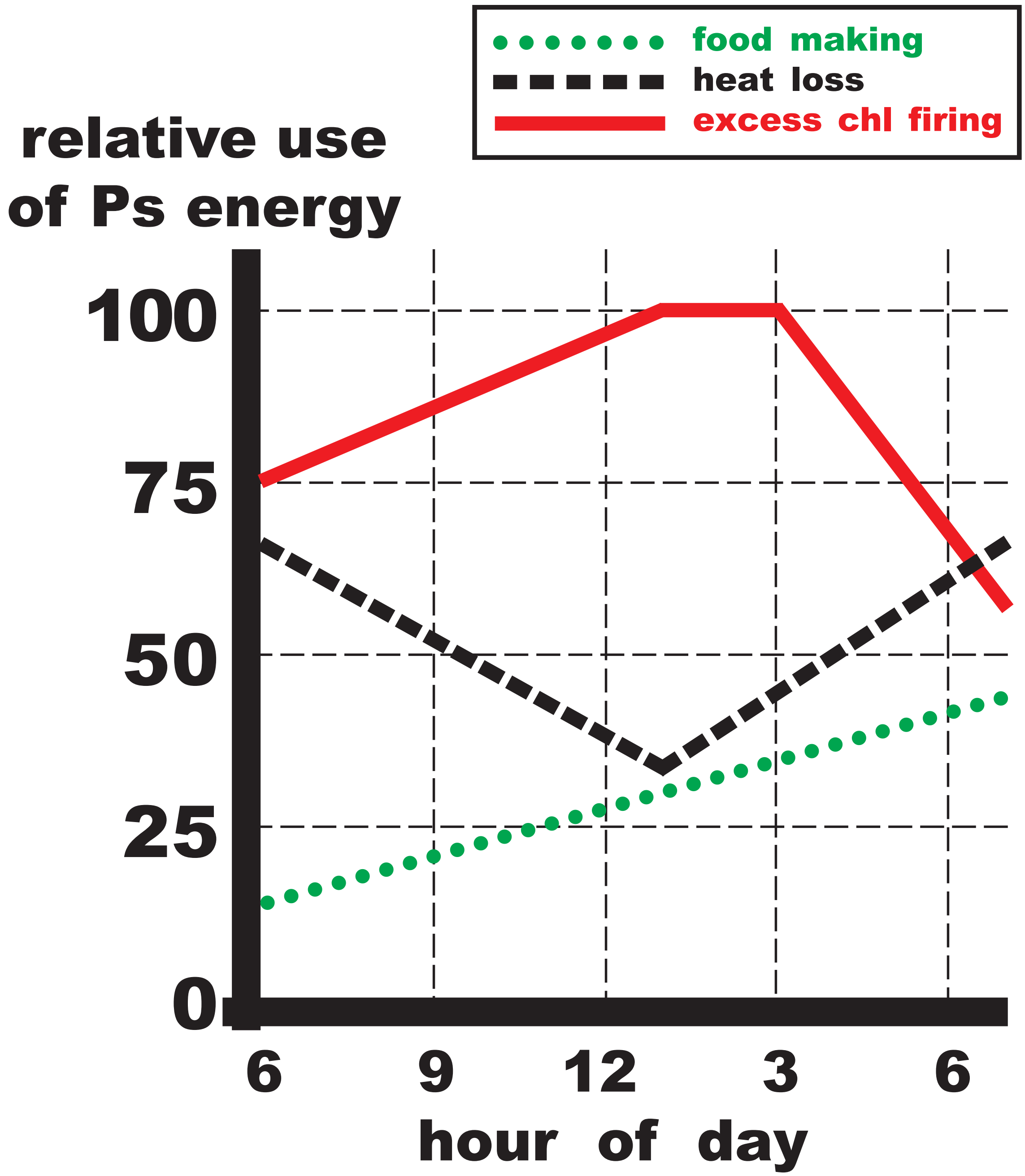

Figure 6: Comparison of light energy use in tree photosynthesis during a day divided among food making, heat loss, and excess chlorophyll firing in LHCII. (derived from Zhang & Gao 1999)

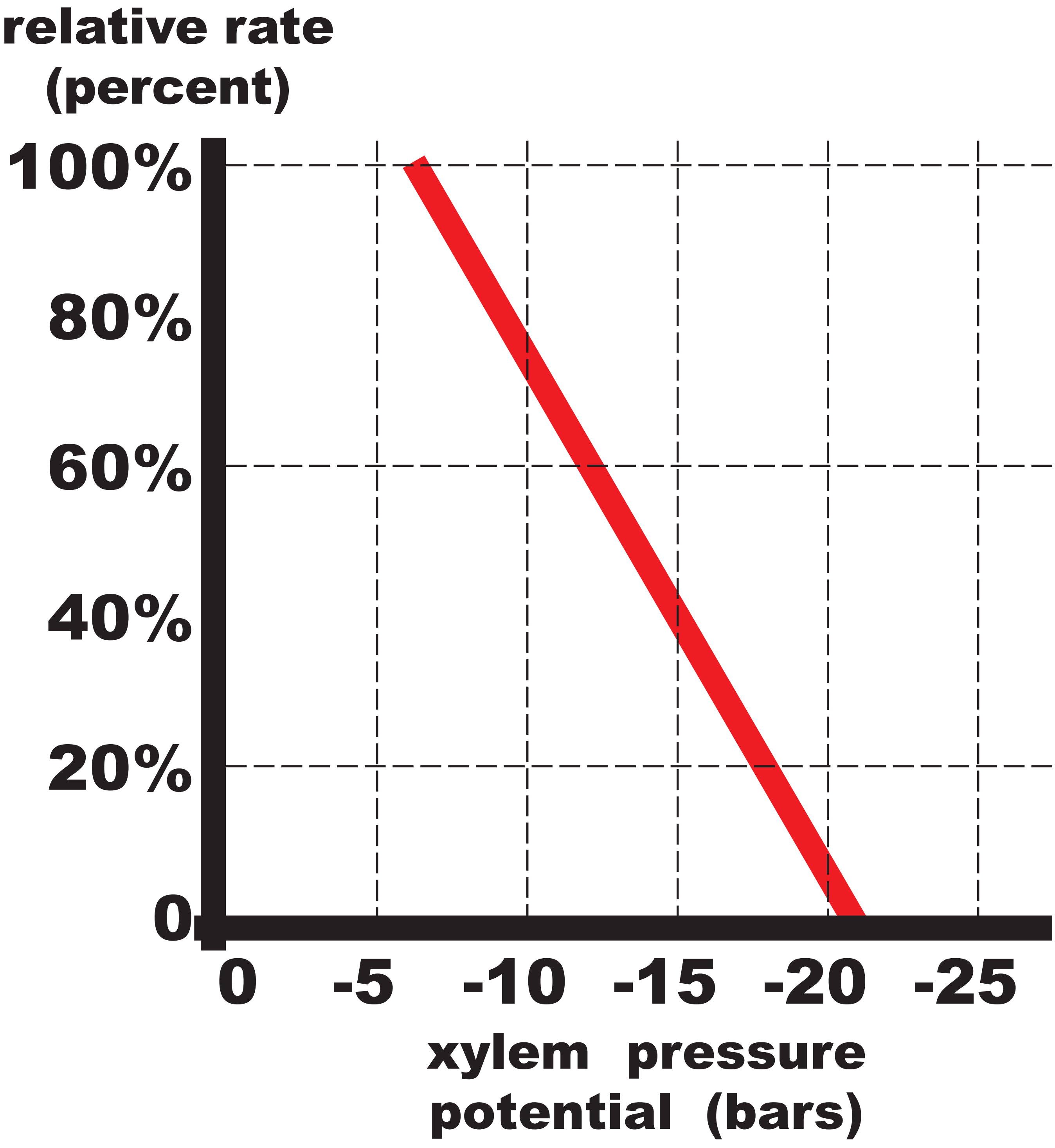

Figure 7: Relative rates of transpiration, net photosynthesis, and stomatal conductance all compared with xylem pressure potential in bars. (from Teskey et. al. 1986)

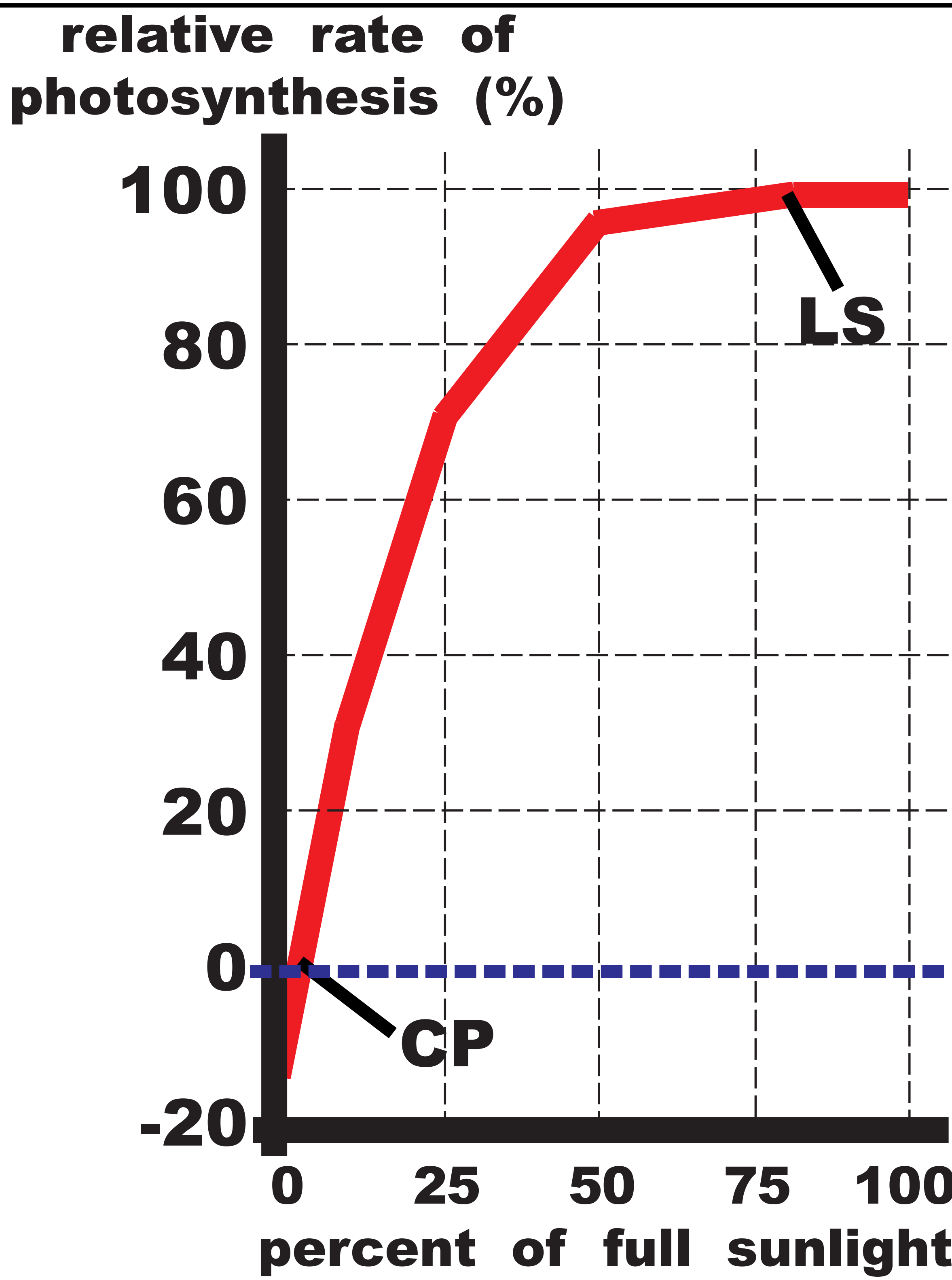

Figure 8: Idealized relative light intensity impact on tree photosynthesis (CO_2 use by Ps & CO_2 loss by Rs) showing light compensation point (CP) and light saturation point (LS).

come. Old leaves will reach a light compensation point at a lower light intensity than young leaves. Young leaves have a greater respiration load from growth. The higher the temperature, the greater light compensation point. Above 85^{o}F (29^{o}C), leaf respiration becomes quite large and photosynthesis is becoming limited by temperature.

Light Sat

As light on a tree continues to increase above its light compensation point, photosynthesis climbs at nearly a constant rate until it begins to reach light saturation. The light saturation point is where more light does not increase photosynthesis. In some shade species more light may cause a decline in photosynthesis. Figure 9 shows photosynthesis differences in sun and shade leaves as light intensity increases per leaf area. Figure 10 shows photosynthesis differences in chlorophyll contents of sun and shade leaves as light intensity increases. Following light intensity increases, suggests a light compensation and saturation points (zones) for both sun and shade leaves.

Leaf Lens

Tree leaves are not simply positioned to intercept light as a two dimensional surface. Leaves are designed to take advantage of light concentration and scattering properties. The epidermis of leaves is clear to visible light and epidermal cell surfaces are usually pushed out into a convex shape. This position, lack of color, and shape causes a light lensing effect.

In sun leaves, palisade cells just under the epidermis have chloroplasts aligned with the light direction. These tightly packed upright cells also act as light guides to channel and scatter sunlight sideways and lower into a leaf. Mesophyll cells with many wet air surfaces also reflect light. The result is average light travel distance through a leaf can exceed leaf thickness by more than 3 times (range = 2-12 times). Chloroplasts may actually be exposed to up to 2-3 times normal light. Shade leaves usually lack palisade cells, where sun leaves of some species may have multiple palisade layers.

Figure 11 shows light in an average leaf from top to bottom through epidermis, palisade, and mesophyll layers of a sun leaf. Light absorption at 680nm, a photosynthetically active wavelength, shows a exponential extinction pattern. The trade-off in the leaf is between mesophyll cells with plenty of CO_2 and palisade cells with plenty of light. Actually, the palisade partially blocks and filters light for mesophyll cells making them more efficient.

Crowns

Photosynthesis in tree crowns quickly declines with crown depth. The more leaves, the greater light extinction down through a crown. Outer and upper leaves usually have a sun leaf structure for capturing high intensity light with a higher light saturation point, while inner and lower leaves tend to have shade leaf structure for more diffuse light and sunfleck capture. Figure 12. Lower, inner marginal branches many times provide few carbohydrates for export. Figure 13 shows how leaf mass per area and nitrogen per leaf area vary with tree height. A tree makes a greater investment in leaves with height. Note individual leaf nitrogen remains roughly the same with increasing height because photosynthesis proteins are required at roughly the same levels in all tree leaves.

Figure 14 shows photosynthesis down through a tree crown. Lower canopy leaves may only be effective around mid-day under high light intensities when upper leaves are inhibited. Figure 15 shows photosynthesis in an upper and lower tree crown. This figure shows the difference during the day, averaged over a season, for photosynthesis. Upper crown position leaves follow general sunlight intensity levels while lower canopy leaves peak quickly around midday.

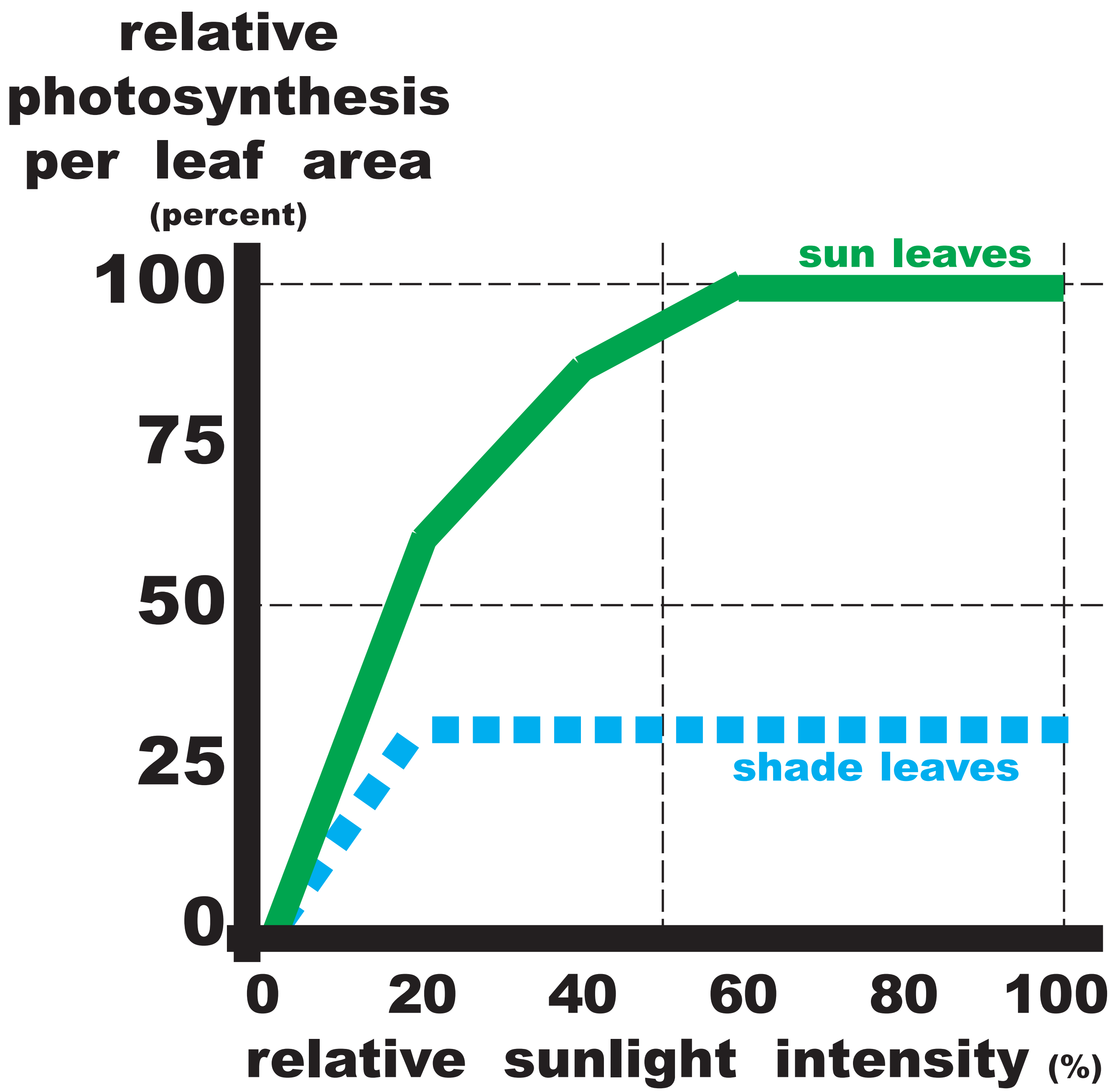

Figure 9: Differences in photosynthesis based upon sun and shade leaf area over different light intensities.
(modified from Lichtenthaler et.al. 1981)

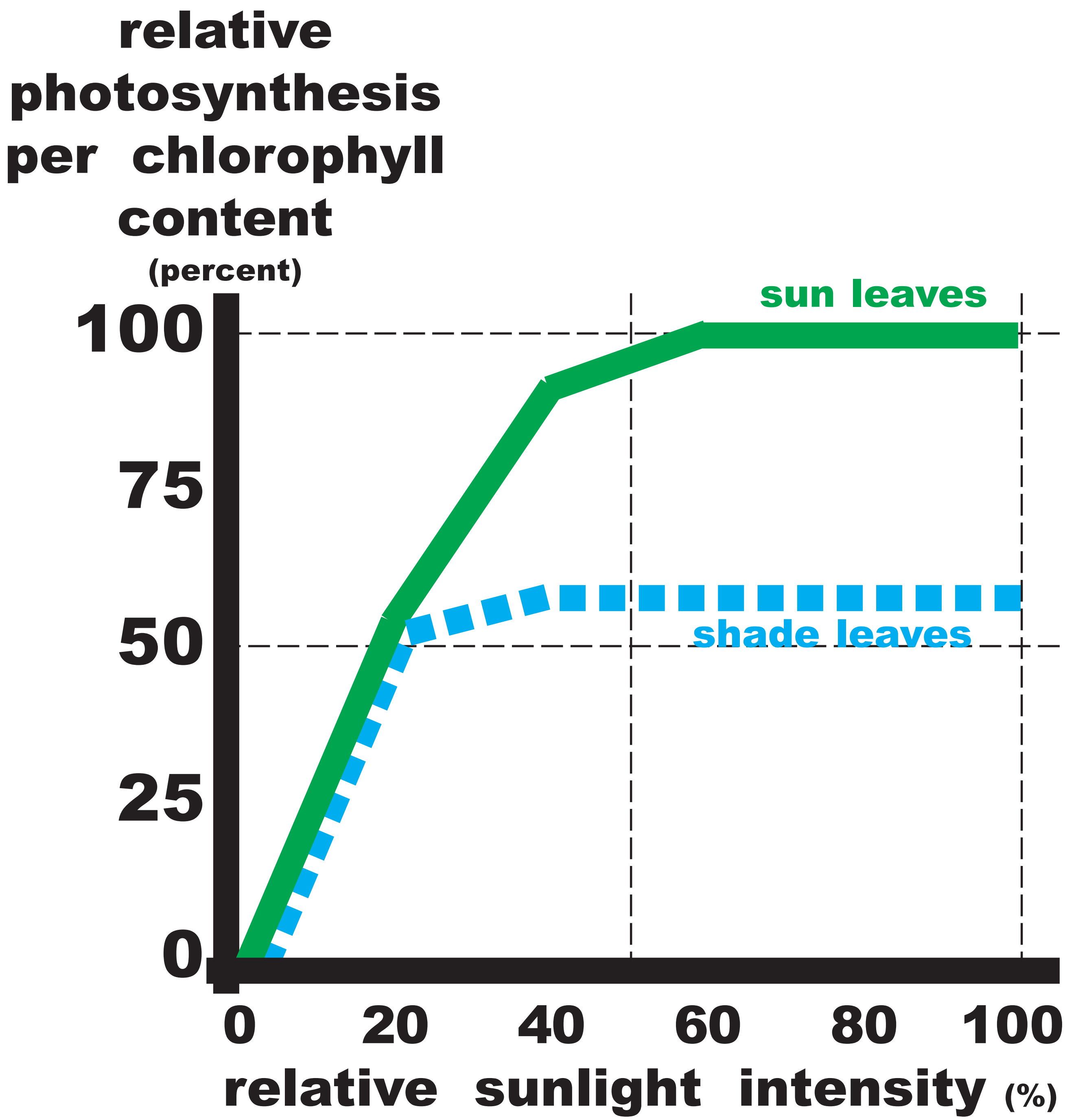

Figure 10: Differences in photosynthesis based upon sun and shade leaf chlorophyll content over different light intensities. (modified from Lichtenthaler et.al. 1981)

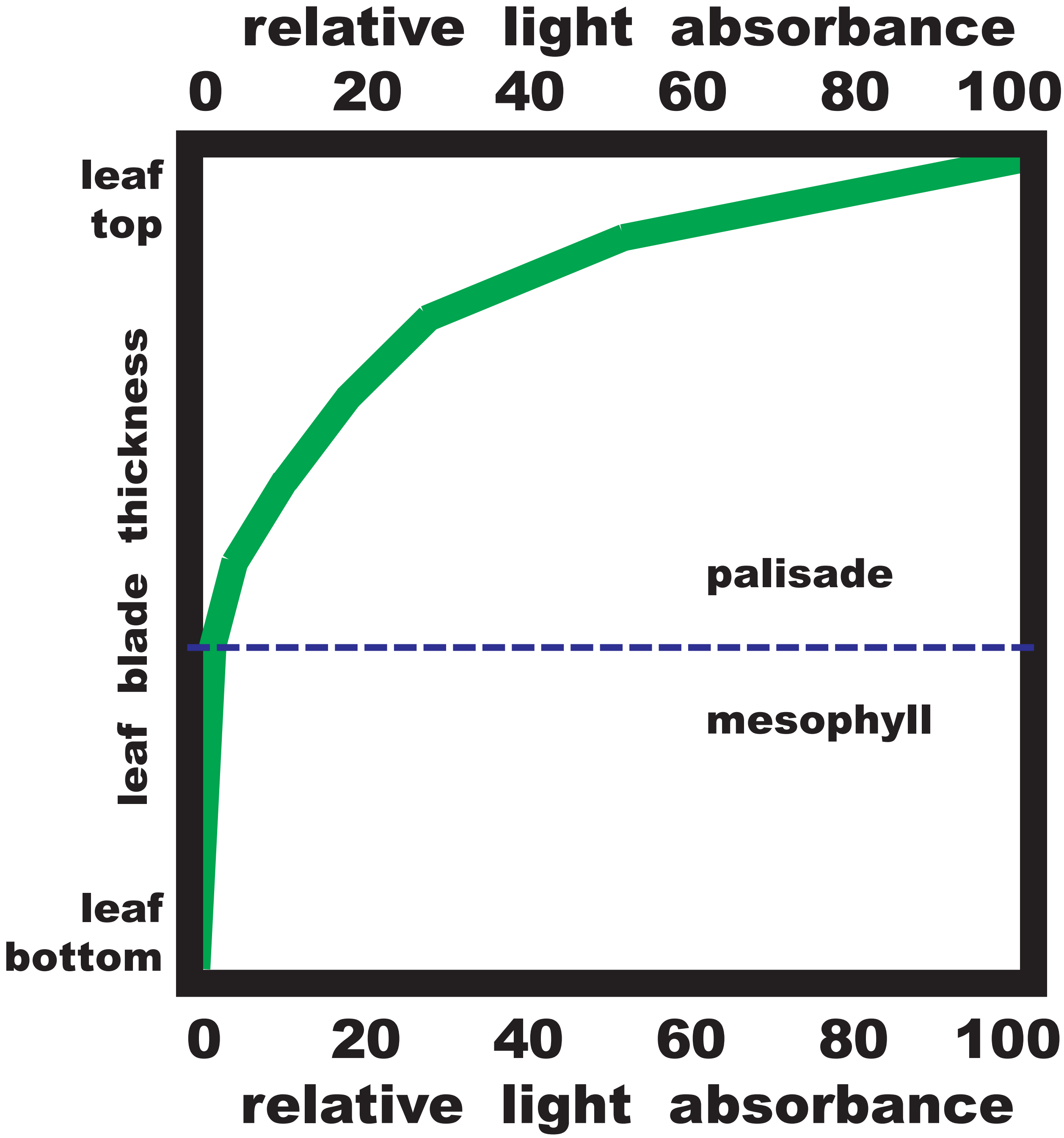

Figure 11: Relative sunlight (red - 680nm) absorbance through a sun leaf. The dotted line represents the mesophyll / palisade boundary.

(from Terashima & Hikosaka 1995)

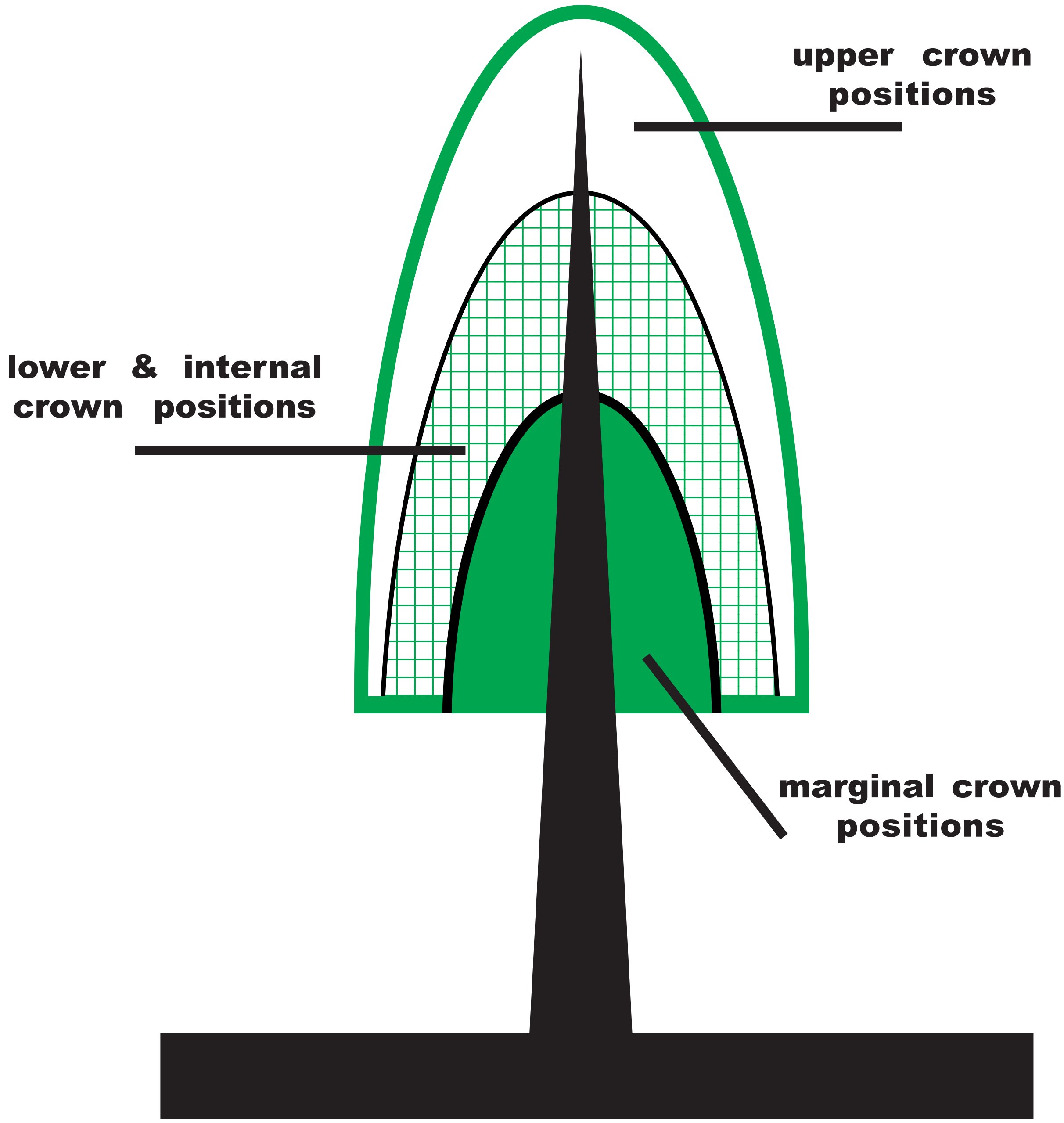

Figure 12: Diagram of crown positions in a tree where different leaf area, leaf productivity, and sapwood volume proportions exist.

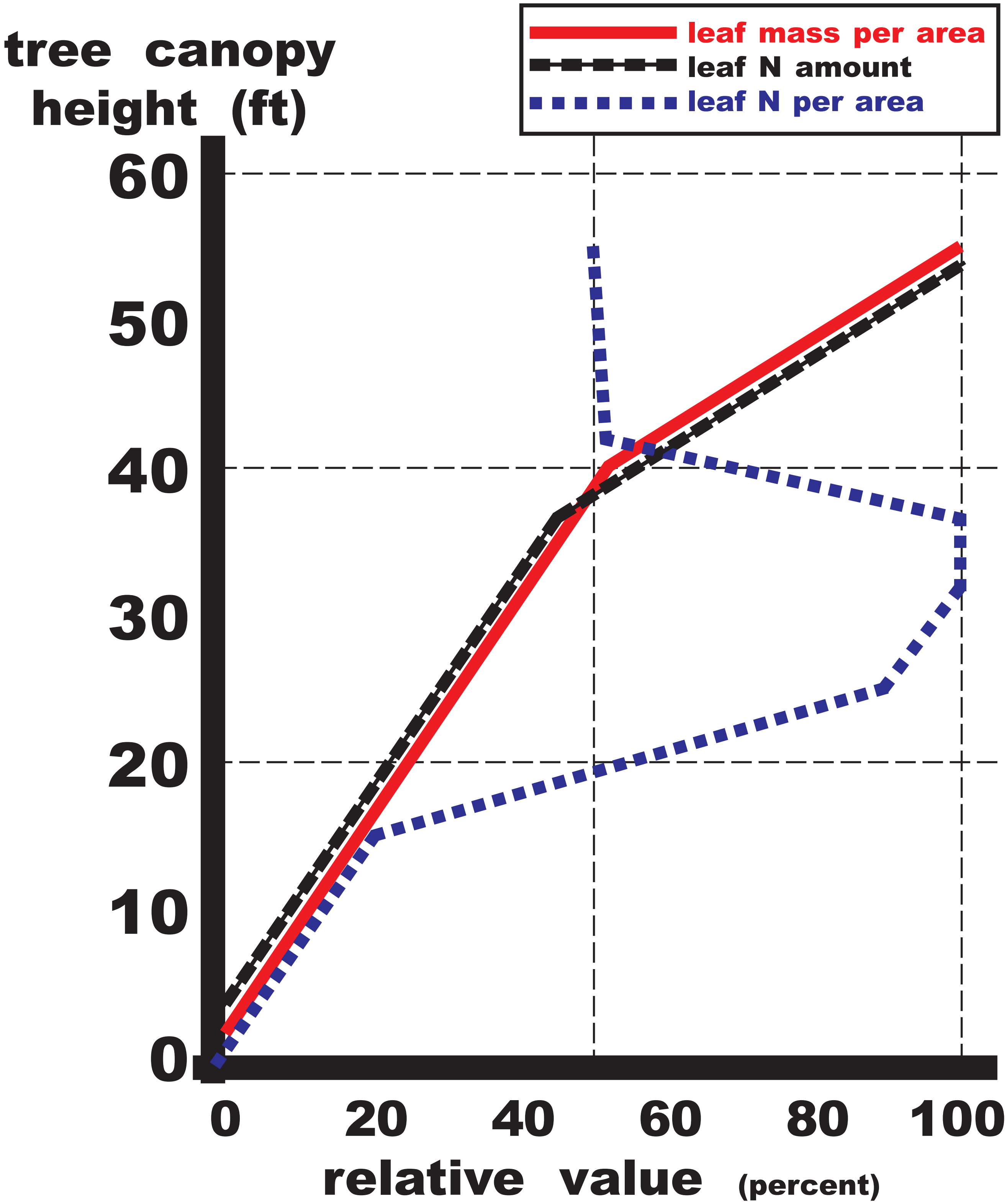

Figure 13: Variation with crown height of leaf mass, leaf nitrogen, and leaf nitrogen per leaf area.
(modified from Ellsworth & Reich 1993)

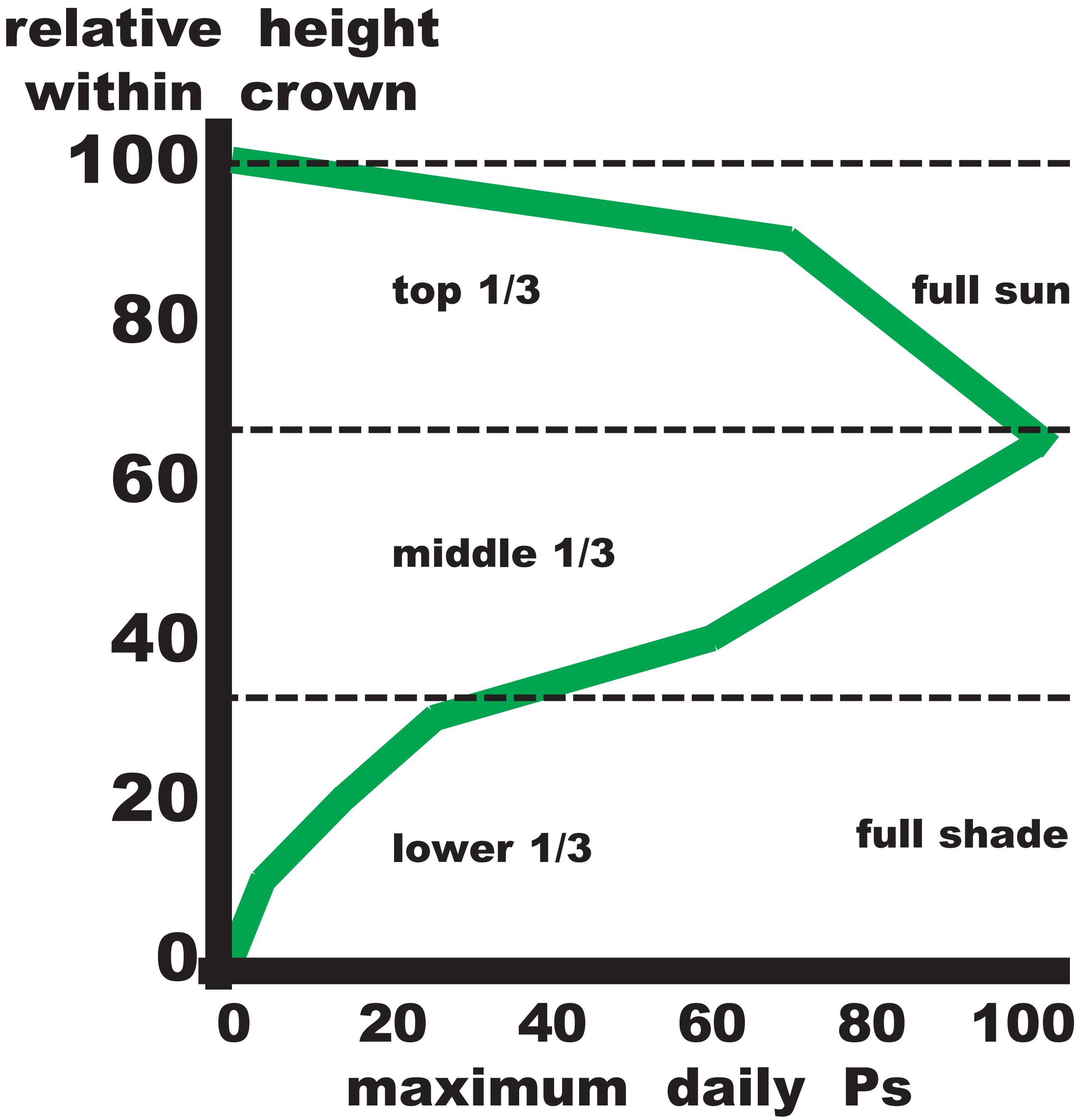

Figure 14: Photosynthesis at different heights in a tree crown. (Woodman 1971)

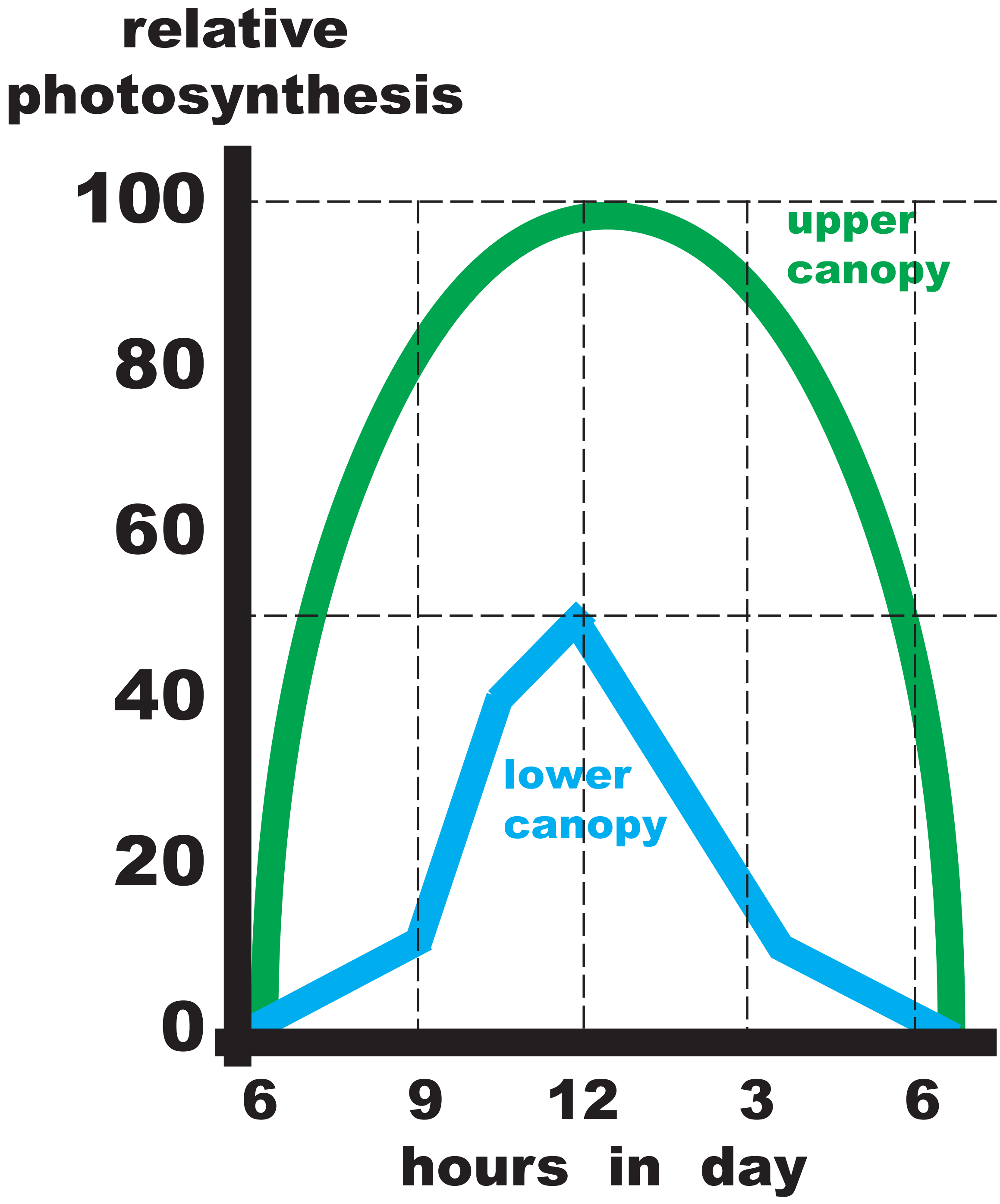

Figure 15: Idealized average daily difference of photosynthesis in trees for upper and lower crown positions. (derived from Marek et.al. 1989)

Effective Leaves

Figure 16 shows the photosynthesis division within an open grown tree crown. The upper third of live crown had 20 - 30% of leaves and 25 - 40% of photosynthesis. The middle third of live crown had 40 - 60% of leaves and 40 - 60% of photosynthesis. The bottom third had 20 - 25% of leaves and 10 - 20% of photosynthesis.

The ratio for percent of crown leaves versus percent photosynthesis in a live crown (called the leaf effectiveness ratio) should be less or equal to one (1.0). A larger value for this ratio symbolizes marginal leaf areas and could suggest pruning options. Trees already shaded by dense foliage and other trees may have a lower third with a ratio approaching 2.0. The upper-most leaf area in some trees may approach a ratio of 0.3.

Shady Leaves

Shade leaves are usually more effective at photosynthesis than sun leaves because shade leaves operate just below the light saturation point and sun leaves are usually light saturated on sunny days and can not use all the light available. Shade leaves also have a lower rate of respiration and so, a lower light compensation point than sun leaves. Figure 17 shows how shade and sun leaves, and shade tolerant and intolerant species, must use roughly the same chlorophyll concentrations under any given light intensity. In Figure 18, note the relative increase in proportional leaf nitrogen for densely shaded leaves. These highly shaded leaves fix less carbon but need more resources. Under nitrogen shortage stress, these leaves would be candidates for senescence.

Sun leaves have a higher photosynthesis capacity than shade leaves. This higher capacity is due to a greater number of chloroplasts, more photosynthetic cells, thicker leaves, thicker palisade cell layer, and greater concentration of Rubisco and carbon fixing materials. These features come at a great respiration cost. Shade leaves do not have as high of maintenance costs as sun leaves. It takes carbon-expensive machinery for photosynthesis. In order to capture a major portion of light and CO2, a leaf will have a major respiration cost in return. Shade leaves with little photosynthesis capacity have less respiration. Figure 19.

Sunflecks

Leaves growing under shade can be completely shaded or live under shade with sunfecking. Sunflecks are near full light intensity for a short duration. If a tree is not near light saturation under shaded conditions, then sunflecks can be valuable. If shade leaves are already tuned for operating near light saturation, additional sunflecks will not have an impact. Upper leaf fluttering, waving, or wilting can change the light environment for lower leaves. Several minutes (3-7 minutes) duration are the minimum needed for effective sunfleck utilization in trees.

Degrees

Temperature has a great impact on photosynthesis and respiration. Photosynthesis is barely present at low temperatures and quickly increases above 40^{o}F (4^{o}C). Photosynthesis reaches a temperature maximum around 70^{o}F (21^{o}C) for temperate species and 85^{o}F (29^{o}C) for tropical trees. Tropical trees may not function well below 55^{o}F (13^{o}C). After photosynthesis temperature maximum is reached, increasing temperatures cause photosynthesis to fall until extinguished around 110^{o}F (43^{o}C). Figure 20 shows a composite temperature curve for photosynthesis in trees divided between average temperate and average tropical species. At higher temperatures, as photosynthesis falls, respiration increases exponentially.

High temperatures can severely damage tree leaves. Above 100^{o}F (38^{o}C) stomates tend to be locked open even in the dark. Membrane adjustments reach biological limits, and membrane permeability changes and becomes unstable. Finally, high temperatures begin to change structures of proteins and denature enzymes.

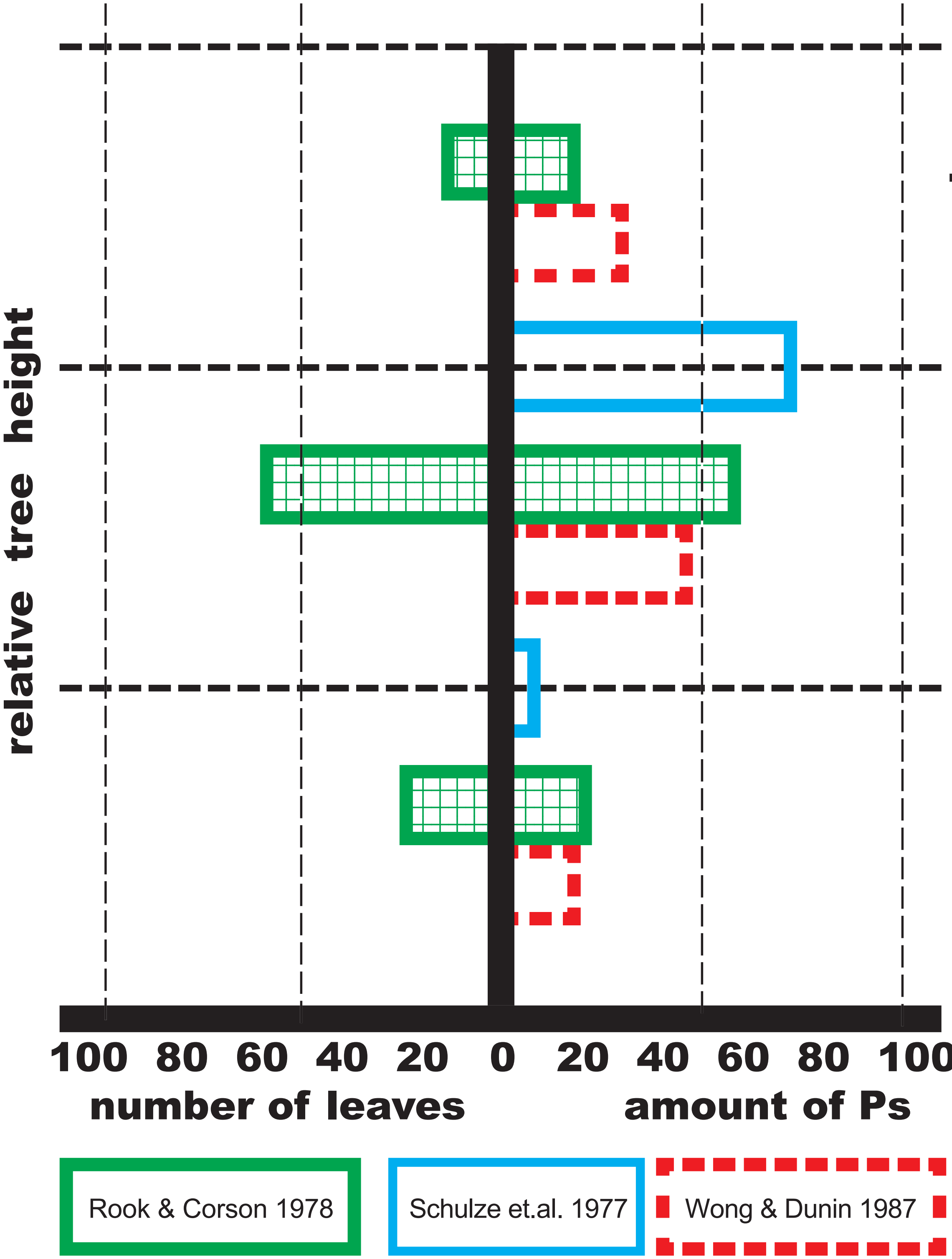

Figure 16: Number of leaves and annual photosynthesis at different heights in tree crowns from three different studies.

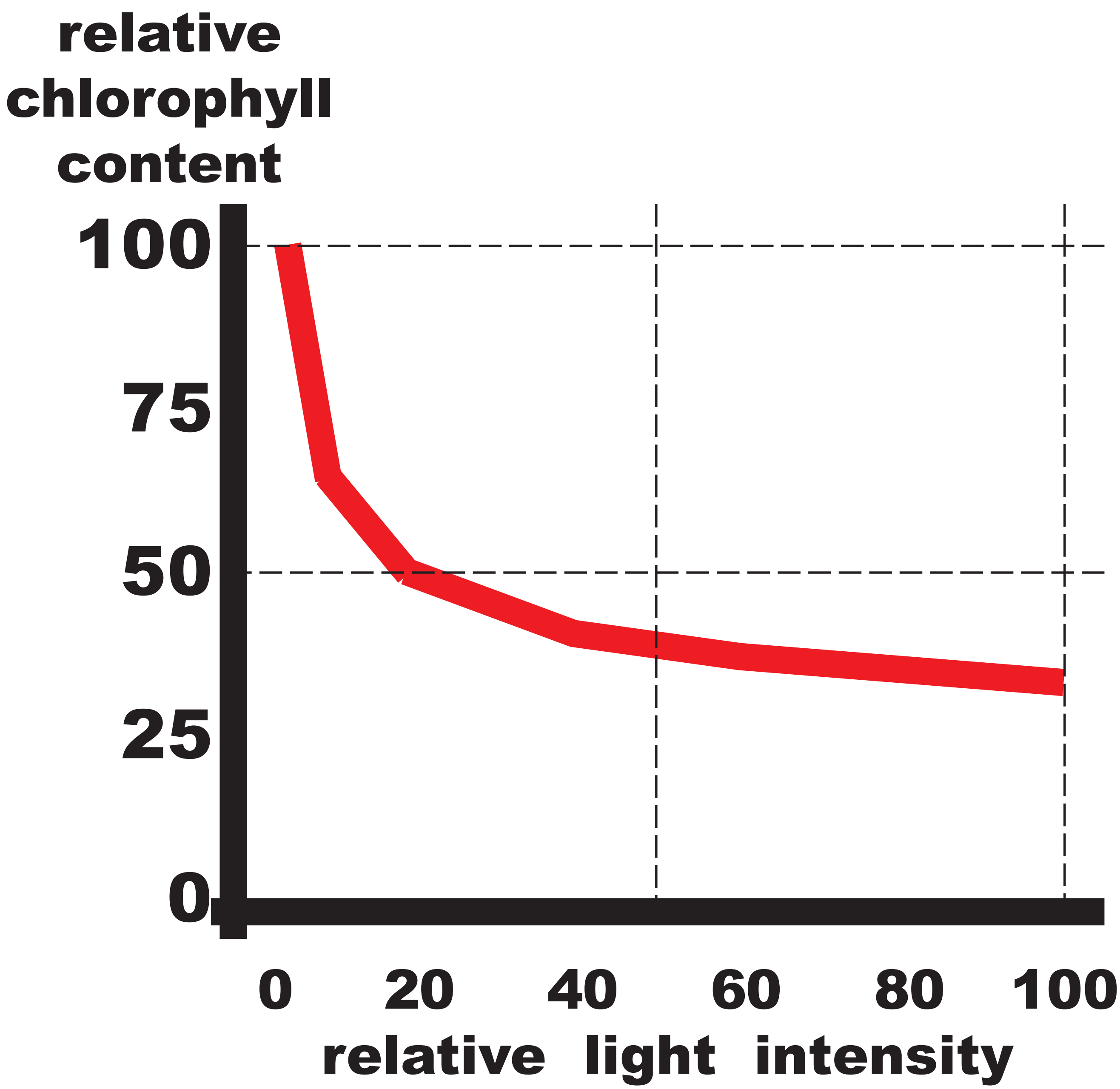

Figure 17: Leaf chlorophyll concentration for both shade tolerant and shade intolerant tree species over different light intensities. (modified from Niinemets et.al. 1998)

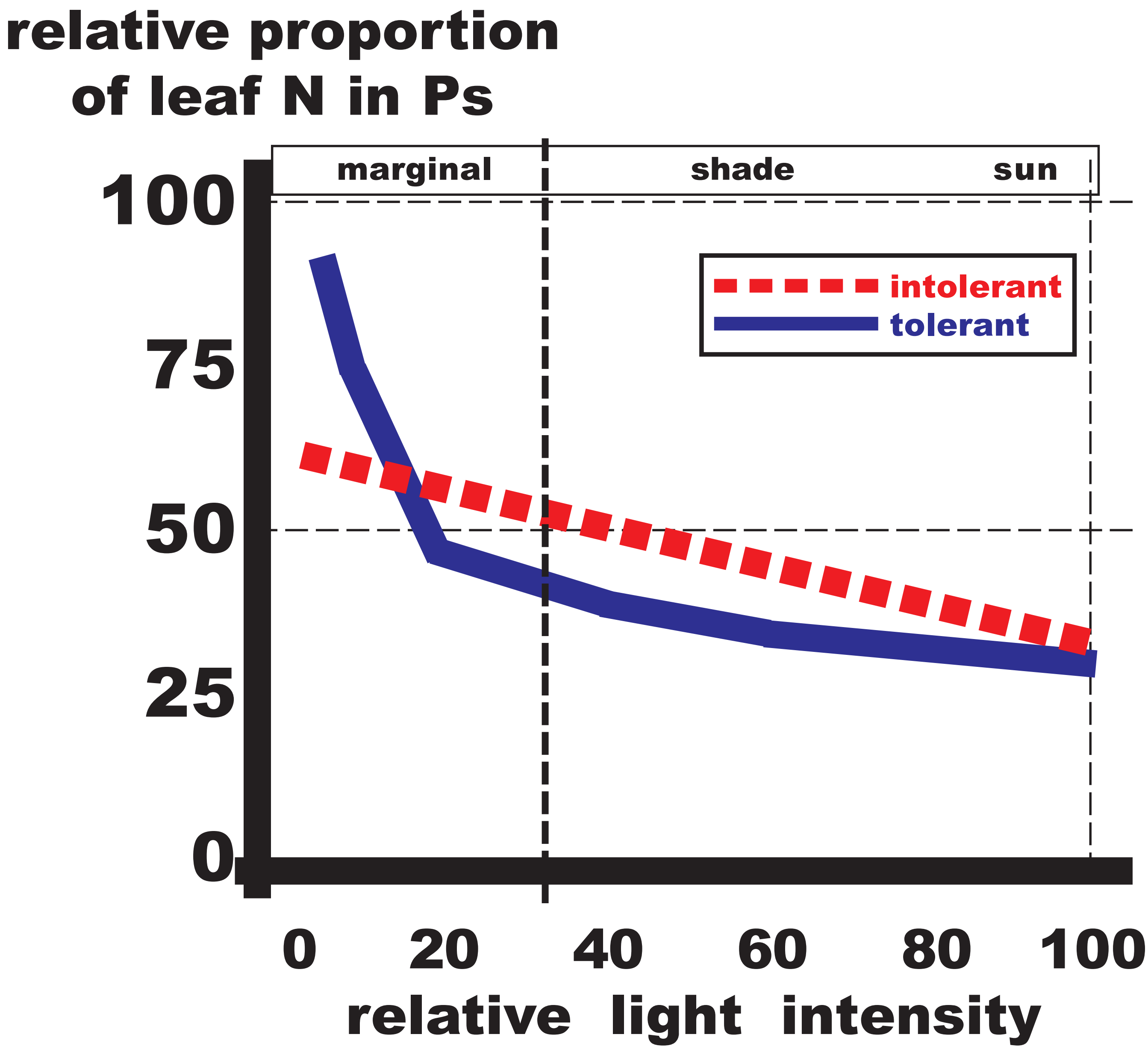

Figure 18: Relative proportion of leaf nitrogen involved with photosynthesis in shade tolerant and shade intolerant tree species over different light intensities.
(modified from Niinemets et.al. 1998)

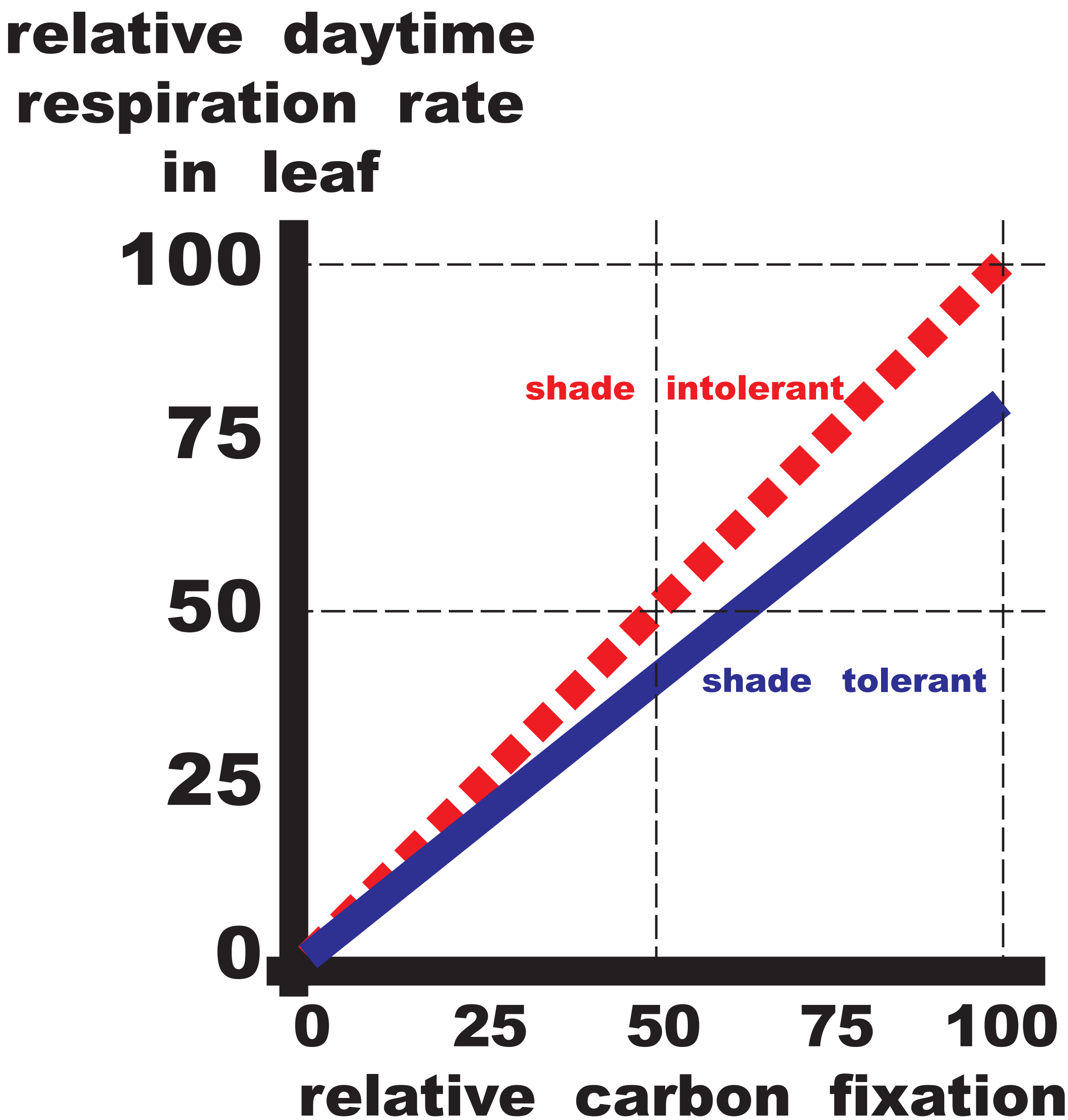

Figure 19: Level of daytime respiration rate in a leaf compared with its carbon fixation rate for shade tolerant and shade intolerant tree species.
(modified from Niinemets et.al. 1998)

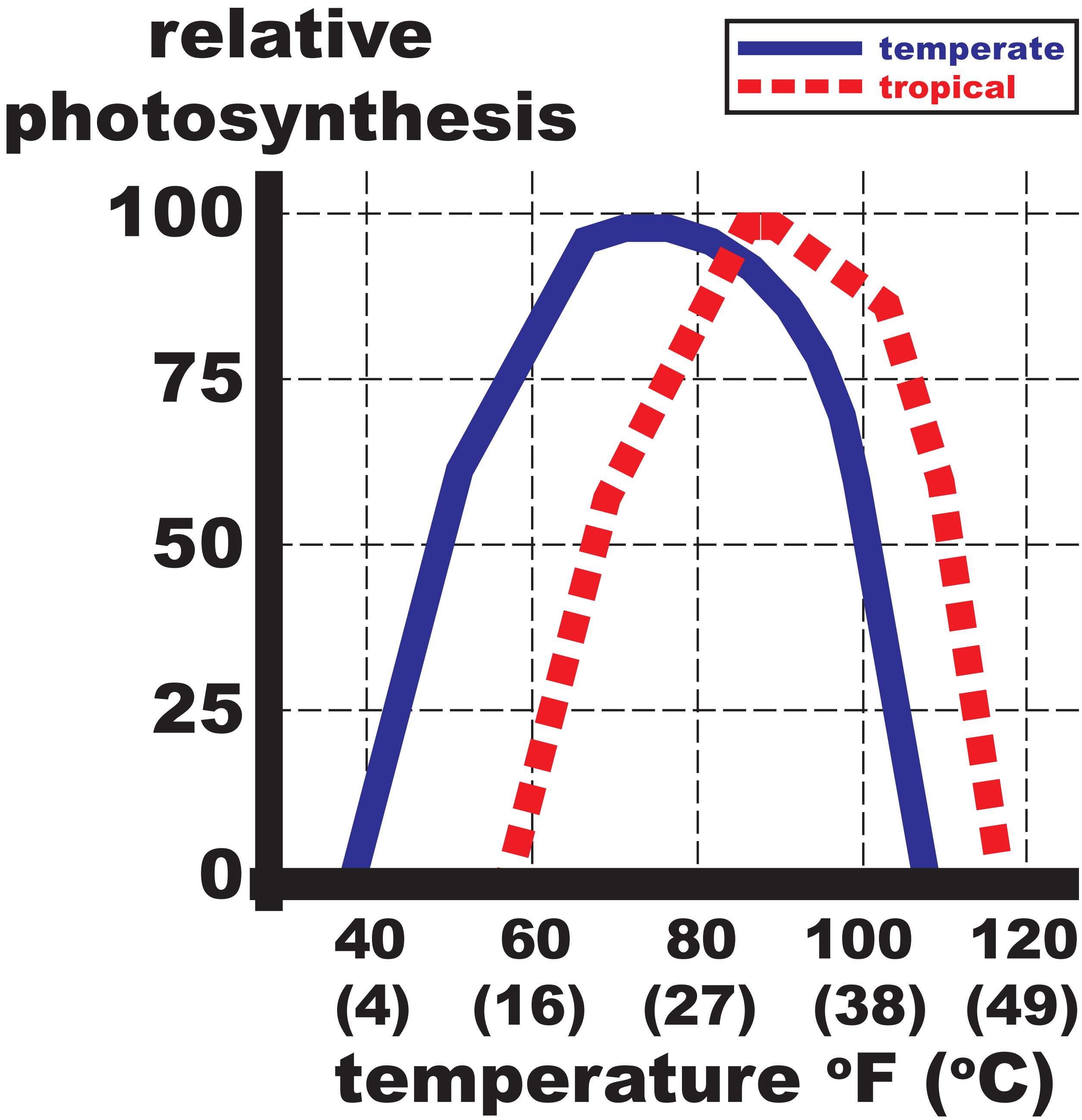

Figure 20: Impact on photosynthesis of temperature for temperate and tropical tree species.
(modified from Larcher 1969)

Hot-N-Cold

Rubisco, and another essential maintenance enzyme, are the first enzymatic systems to be damaged by heat. Heat shock proteins are produced to hold other essential proteins together. Figure 21 shows the percent loss of photosynthesis capacity with exposure to elevated temperatures. The recovery times lengthens 2 weeks longer with every 1°F (0.55°C) degree increase over a high heat base temperature.

Cold temperatures cause inhibition of electron transfer, ATP production and use, CO2 carbon fixation, and the Calvin cycle. Light continues to cause chlorophylls to fire and generate damaging materials. Light harvesting center II (LHCII) is three times slower than LHCI at low temperatures. Tree response to low temperatures include decreasing chlorophyll antenna size, less LHCII, and poor maintenance of the xanthophyll cycle for electron quenching.

Water

Water deficits can lead to stomate closure and photosynthesis decline. Stomate closing is very sensitive in some tree species to root growth regulator messages representing soil water tensions. One growth regulator placed in the water stream is ABA (abscisic acid). As water deficits continue to increase, chlorophyll breaks apart and free magnesium ions can damage cell contents. The carbon fixation process and ATP production are also very sensitive to water shortages in a leaf.

Elements

Essential element shortages can inhibit photosynthesis and respiration in trees. Nitrogen (N) is in great demand by all aspects of photosynthesis. Less clear cut, but nearly as important is total leaf phosphorus (P). Sulfur (S) is required for some proteins and for cytochrome (CYTO). Iron (Fe) is required for chlorophyll synthesis, FERD, and CYTO. Manganese (Mn), calcium (Ca), and chlorine (Cl) are required for oxygen release in photosynthesis, and are needed to sustain several enzyme system. Copper (Cu) is needed for plastocyanin (PC) in the electron transfer chain. Both copper and zinc (Zn) shortages can decrease photosynthesis by 25-50% before any visible sign of damage can be seen in the leaves.

Element enrichment to correct whole tree deficiencies, and irrigation to relieve water deficits, stimulate photosynthesis. Excess fertilization, especially with nitrogen, can slow photosynthesis. Excess water, poor drainage, and anaerobic soil conditions can greatly limit photosynthesis and disrupt normal respiration. Anaerobic respiration causes damaging materials to be produced and accumulated, with greatly reduced energy generated.

Killing Places

A number of herbicides attack different places in the light capture process leading to damage and death of trees. For example, norflurazan stops carotenoid production and causes leaves to bleach white. Atrazine and diuron prevents PQ from functioning overloading the LHCII system and generating damaging high energy materials. Paraquat diverts energy from transferring to FERD, and instead generates highly damaging peroxides in chloroplasts.

Respiring Types

There are three purposes for respiration in trees: growth, maintenance, and waste. Growth respiration powers meristem division and expansion. Maintenance respiration sustains life among living tree cells. Waste respiration breaks apart carbon bonds with no energy conserved, or produces unusable materials. Generally, maintenance respiration accounts for 80%, growth respiration for 19%, and waste respiration for 1% of total carbon respired in trees. These values differ by tree age, species, and environmental stress palette. Figure 22.

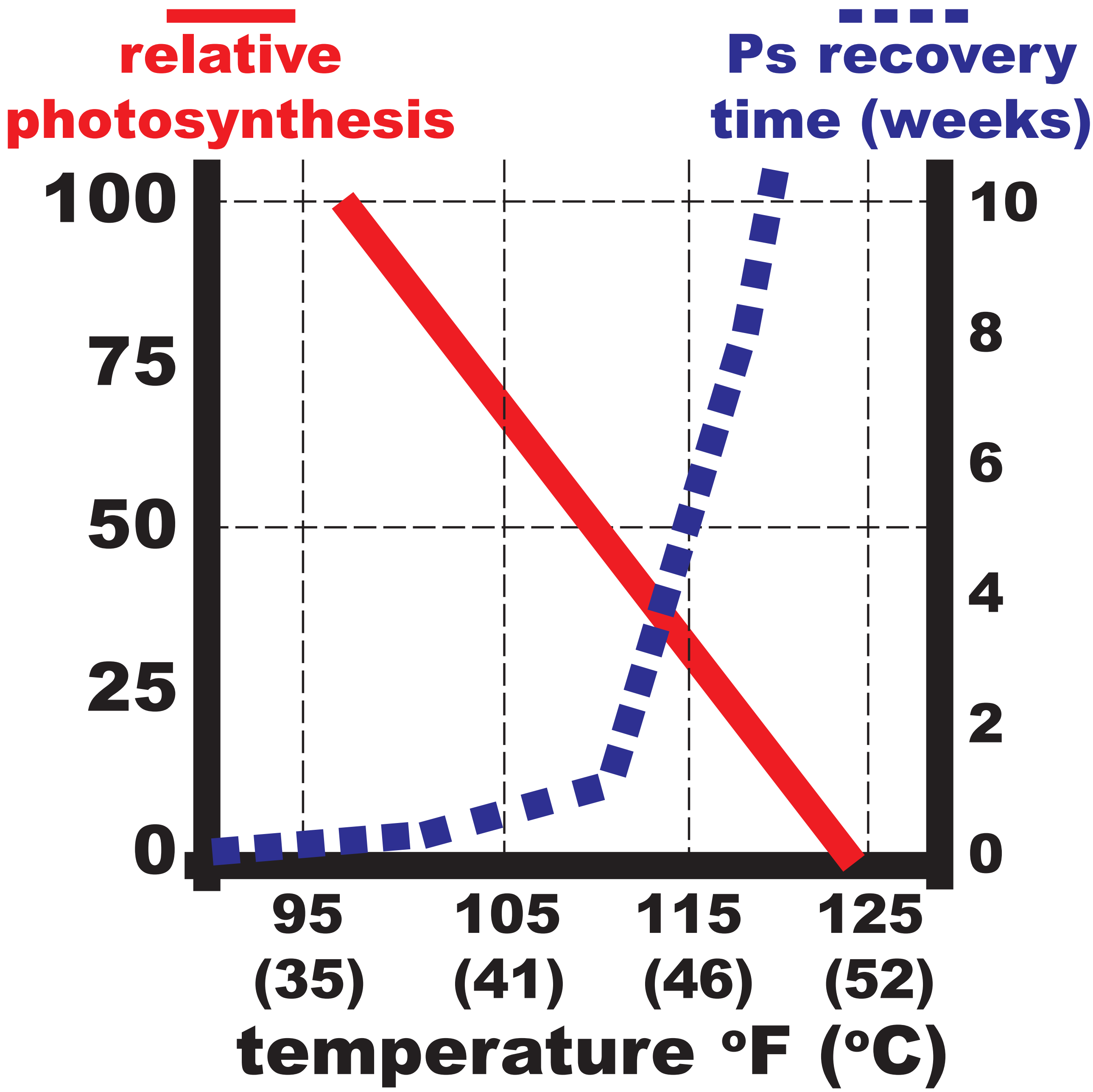

Figure 21: Idealized photosynthesis impact from high temperature exposure (solid line) and associated recovery time in weeks at 68°F (20°C) (dotted line).
(derived from Berry & Bjorkman, 1980)

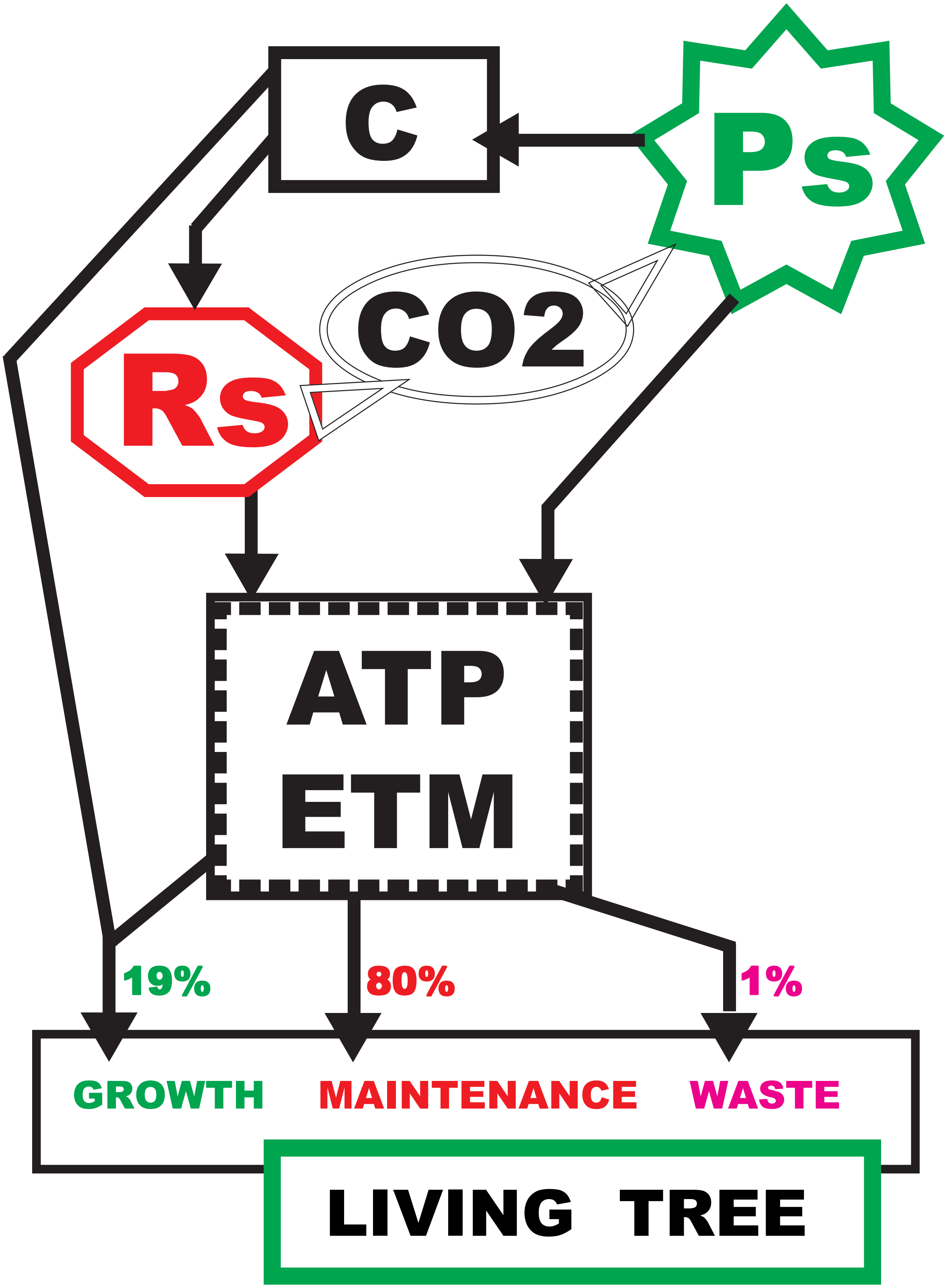

Figure 22: Tree life functions centered around respiration and its associated energy production.

How Much?

Young trees use ~33% of their daily photosynthesis for respiration, and this percentage climbs with tree age. Older trees have progressively less photosynthetic production for an increasing volume of respiring tissue. One calculation showed in topical forests with hot nights, 75% of photosynthetic productivity is lost to respiration.

The greater growth rates, the greater respiration rates. Tree parts listed in decreasing order of respiration rates are: expanding buds, leaf expansion points, meristems areas, twigs, roots, stems, and aging / senescing tissues. For example, Figure 23 shows the annual pattern of respiration among tree tissues. Leaves are by far the greatest respiring tissue in trees accounting for more than 60% of total tree respiration. Leaf respiration tends to decline with age, with lower crown positions, and in shade leaves.

Woody Parts

Respiration rates in twigs, branches and stems vary by tissue age and temperature. Young twigs with a large proportion of living tissue have the greatest respiration of above ground structural parts. In stems and branches, most respiration occurs in phloem and xylem next to the vascular cambium, accounting for as much as 50% of total respiration load. Respiration in trunks is directly related to the number of living cells and temperature when a tree is not dormant.

In a stem cross-section, respiration drops as the first annual increment is passed and continues to decline as the sapwood / heartwood boundary is approached. For example, Figure 24 shows respiration rates changes from outside at the periderm to inside at the heartwood in a tree. The area on either side of the cambium where new cells are being developed represent the peak of respiration in a tree stem.

Total root respiration is dominated by absorbing root processes (75%), and interactions with mycorrhizal fungi (20%) and other soil organism interactions like nodule respiration. In addition, daily temperature buffering in soil places peaks of root respiration out of sink with crown respiration.

Life Aids

All living cells in trees respire. One means to estimate respiration load, and so volume of living cells, is by measuring sapwood area. Sapwood is around the outside of a tree cross-section representing tissue with living and dead cells. Figure 25. Sapwood with living cells is contrasted with heartwood, the central core of a tree containing no living cells. Heartwood core volume accumulation is accelerated and slowed depending upon tree stress. Sapwood is an easily measured component of multiple year stress impacts on diameter growth. Figure 26 shows combinations of sapwood and heartwood volume growth and cross-section expansion, integrating environmental constraints.

If depth of the sapwood / heartwood transition is determined for any stem location below the live crown, sapwood area represents an approximation of relative living cell volume above. Sapwood area is used by foresters and tree health care providers to understand growth and health changes in a tree. Figure 27 provides an estimate of sapwood area in square inches of a stem or branch of a given diameter in inches and various radial depths of sapwood in inches. This depth could be measured with an increment core.

For example, a 15 inch diameter tree would have a sapwood area of 177 square inches if it was 100% sapwood, but only 44 square inches if sapwood was only one inch cross-sectional radius in depth. Since sapwood area approximates respiration loads in trees, the difference of sapwood area (and associated respiration load) in this example is 4X. Sapwood area has been used to measure pruning overdose values in trees, as in the Coder Sapwood Area Pruning Dose Assessment. Figure 28A & Figure 28B.

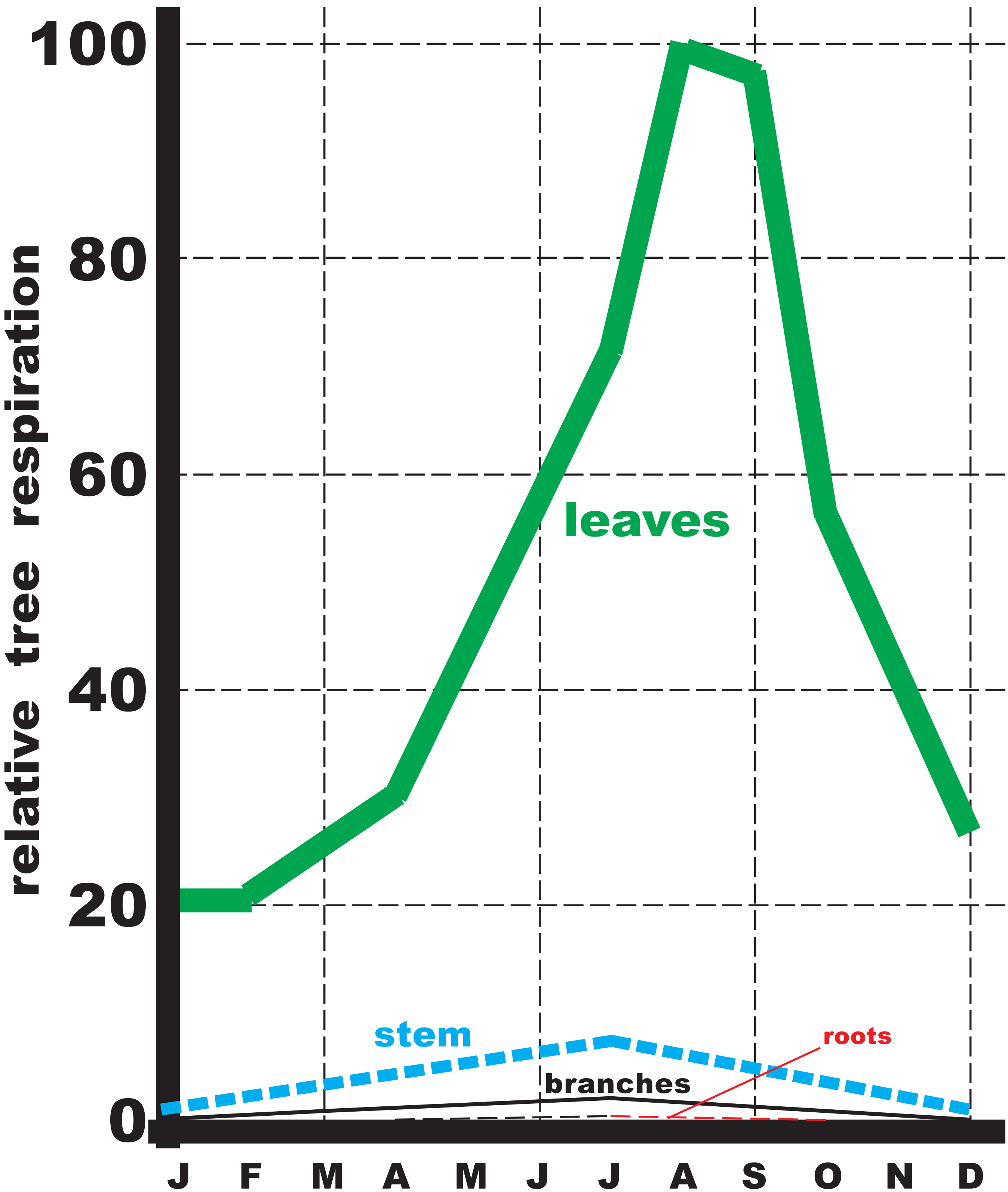

Figure 23: Annual pattern of relative respiration for an evergreen tree. (after Kinerson 1975)

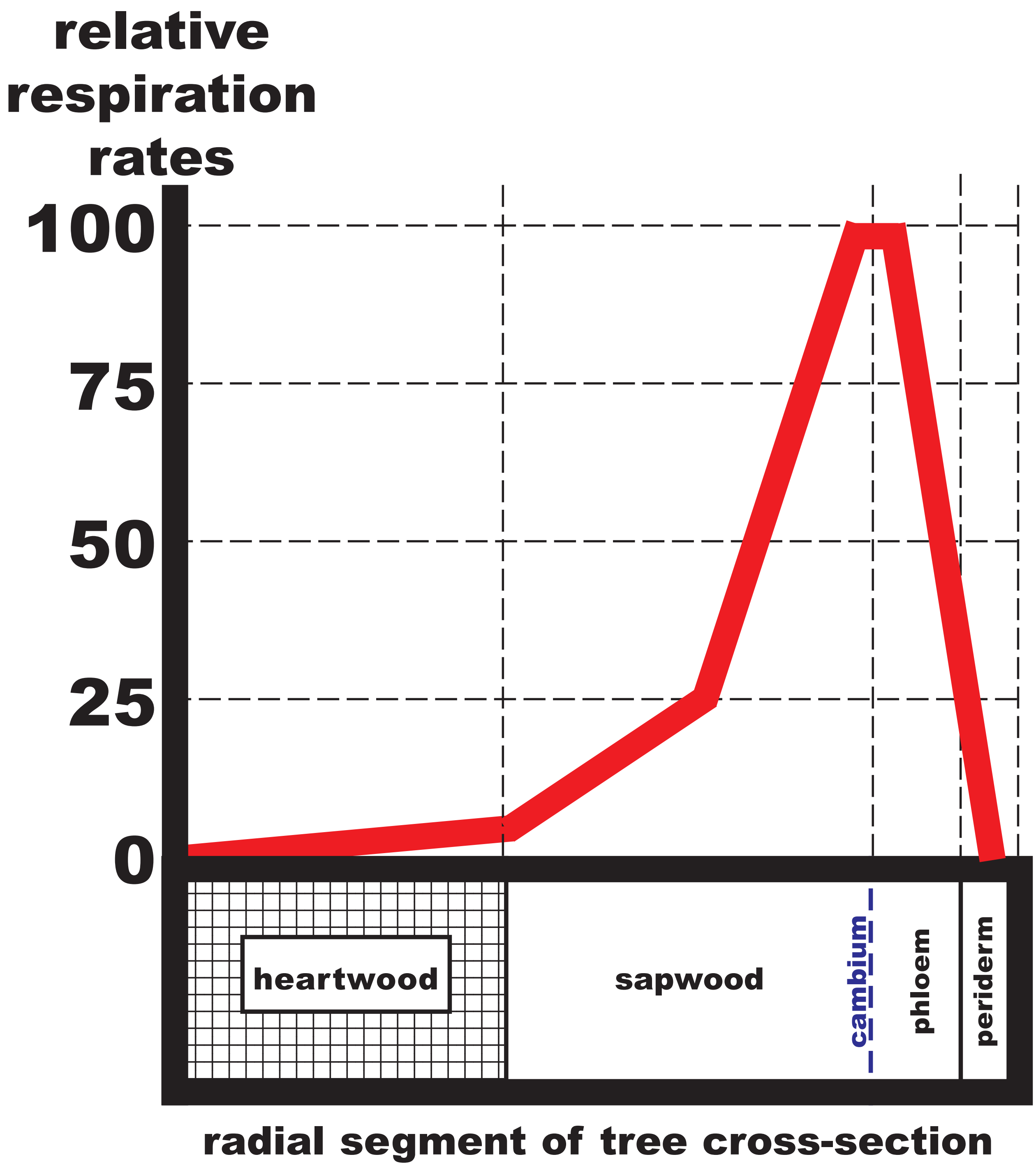

Figure 24: Respiration rates along a tree stem cross-section radius. (not to scale)
(from Goodwin & Goddard 1940)

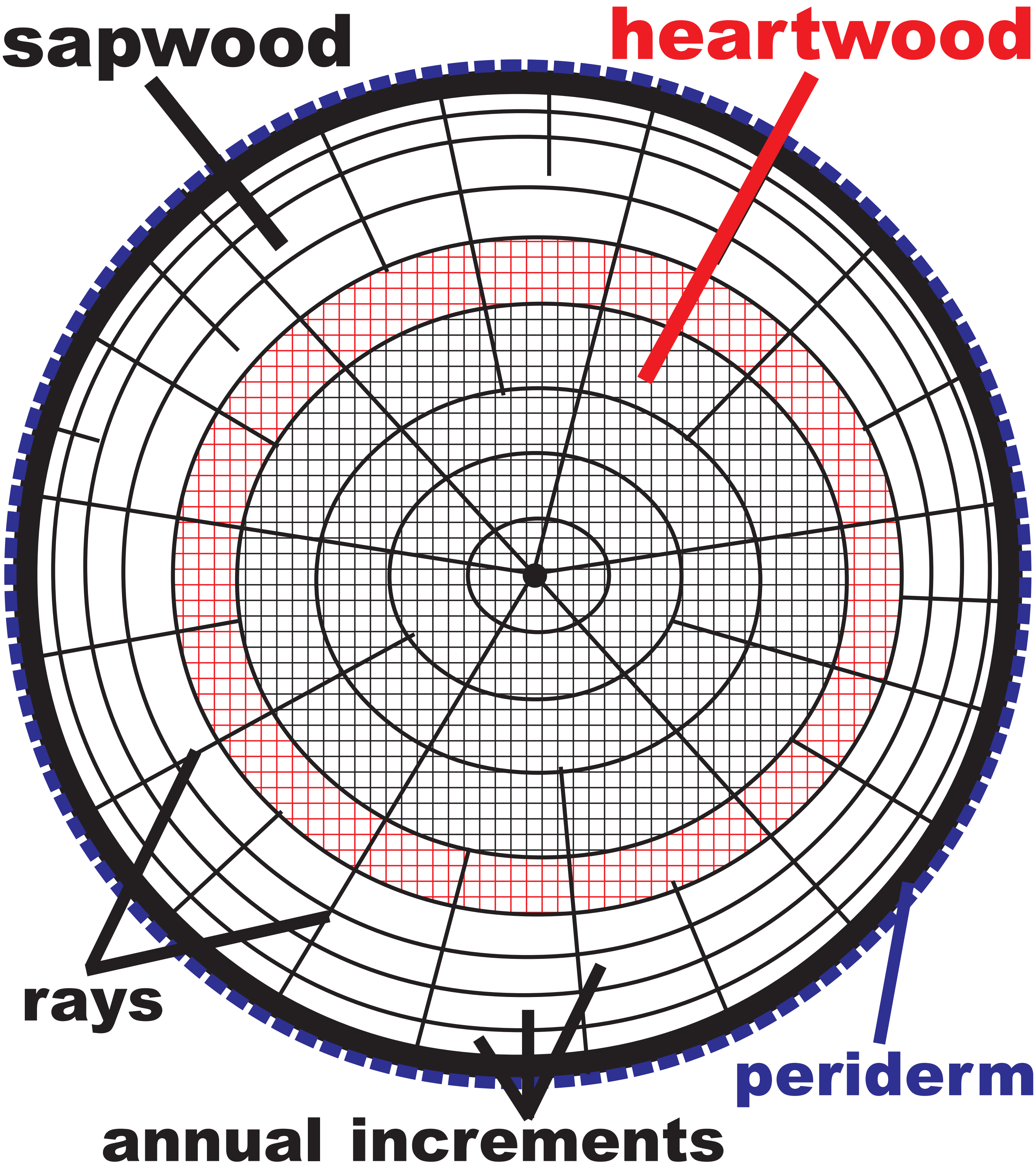

Figure 25: Diagram of a stem cross-section showing sapwood and heartwood (shaded).

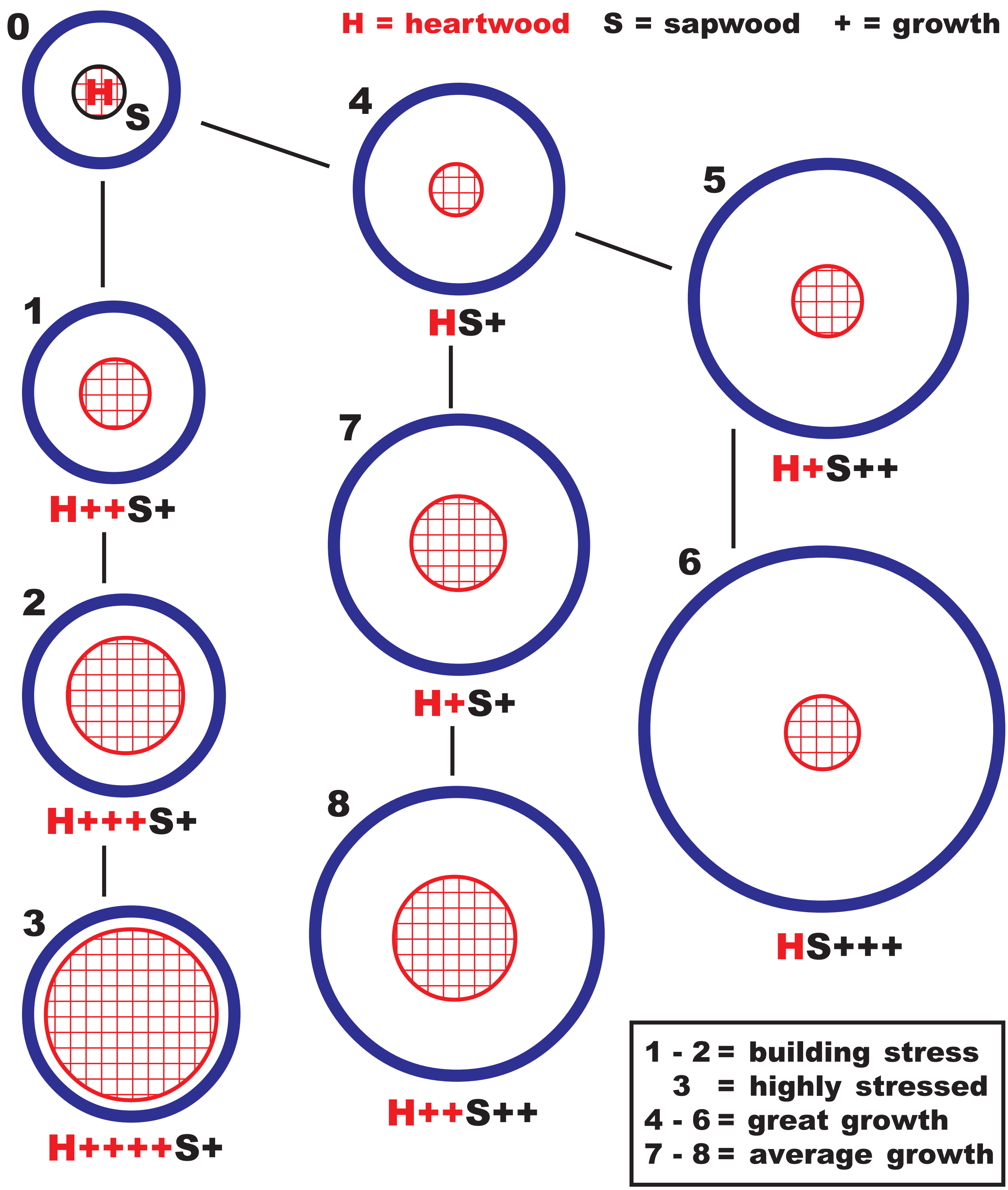

Figure 26: Diagram showing various cross-sectional sapwood and heartwood expansion and growth combinations representing different environmental constraints on trees.

diameter (inches)	sapwood depth to heartwood (inches) 0.5"	1"	1.5"	2"	2.5"	3"	3.5"	4"	100% sapwood
0.2 in									0.03
0.4									0.13
0.6									0.28
0.8	--								0.5
1	--	--							0.8
2	2 in^2	--	--						3
3	4	6	--	--					7
4	6	10	3	--	--				13
5	7	13	17	19	--	--			20
6	8	15	21	25	27	--	--		28
7	11	19	26	32	36	38	--	--	39
8	11	22	30	37	43	47	49	--	50
9	14	25	36	44	51	57	61	63	64
10	15	29	40	51	59	66	72	76	79
11	16	31	45	56	67	75	82	88	95
12	18	34	49	63	74	85	93	100	113
13	20	38	54	69	83	94	105	113	133
14	21	41	59	75	90	104	115	126	154
15	23	44	64	82	98	113	127	138	177
16	24	47	68	88	106	122	137	151	201
17	26	50	73	94	114	132	148	163	227
18	27	53	77	100	121	141	159	175	254
19	29	56	82	106	129	150	170	188	283
20	31	60	87	113	137	160	181	201	314
21	32	63	92	119	145	169	192	213	346
22	34	66	97	126	153	179	203	226	380
23	35	69	101	132	161	188	214	238	415
24	37	72	106	138	169	198	225	251	452
25	39	76	111	145	177	208	237	264	491 in^2

Figure 27: Sapwood cross-sectional area in square inches for stem diameters (in) at various sapwood radial depths (in).

Coder Sapwood Area Pruning Dose Assessment

tree sapwood area in square inches X 0.334

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sum of all
[branch sapwood area pruned X crown position value]

crown position values:
1 = <2 year old sprouts -- any crown location
2 = lowest & internal crown positions
3 = highest crown positions

=

PRUNING CYCLE DOSE or PCD

> 1.0 = within biological limits
< 1.0 = exceeded biological limits -- pruning stress

Figure 28A: Example assessment of pruning dose for one tree per pruning cycle based upon sapwood area measures.
(example on next page -- Figure 28B)

Coder Sapwood Area Pruning Dose Assessment

Example: 10" diameter tree (DBH)

diameter branch pruned	sapwood area	crown position	crown position value	calculated values
3"	7	low	2	14
2"	3	low	2	6
1"	.8	low	2	1.6
1"	.8	high	3	2.4
0.6"	.28	high	3	0.84
0.4"	.13	sprout	1	0.13
			[sum of all =	23.37 in^2]

If tree is:

100% sapwood tree =
pruning cycle dose = 1.13 (13% underdose)

3" sapwood in tree =
pruning cycle dose = 0.94 (6% overdose)

1" sapwood in tree =
pruning cycle dose = 0.41 (59% overdose)

Figure 28B: Example assessment of pruning dose for one tree per pruning cycle based upon sapwood area measures.
(continuation of Figure 28A on previous page)

Got More – Use More

One impact on tree respiration is having enough carbohydrate to respire. The more food in a tree part, the more it tends to respire. Young leaves, phloem, and cambium-adjacent parenchyma have very high respiration rates. Upper canopy leaves respire more than lower canopy leaves partially because of a greater supply of photosynthate available.

Interestingly, moving, bending, rubbing, and handling tree tissues tend to significantly increase respiration. This respiration load increase may be associated with micro-fractures and cell-to-cell breaks within living tissue. Wounding and associated compartmentalization process greatly increase respiration in any living cells which remain undamaged nearby. Periderm production and wound periderm setting also generate significant respiration loads.

Temperature

As temperature increases, respiration climbs exponentially until proteins are denatured and life crashes. Respiration tends to peak between 105 - 120^{o}F (41 - 49^{o}C). Figure 29. Generally, respiration rates double for every 18^{o}F (10^{o}C) increase in temperature, starting at 40^{o}F (4^{o}C) where water is densest. Figure 30 shows the multiplier effect of temperature on respiration. Respiration capacity is increased in trees over the long run with cold, not freezing temperatures.

Conclusions

Tree photosynthesis and respiration are complex biochemical reactions occurring within a specialized cellular environment. A tree extracts and conserves a great amount of energy from a hostile environment.

A tree effectively:
– captures a small portion of massive light energy striking tissues every second;
– provides a pathway for CO2 to enter where it can be processed;
– produces carbon centered materials which can be used for life processes and transported to all living tissues; and finally,
– uses our highly oxidative environment to bleed off electrons and protons slowly, while encumbering a good portion of their available energy.

These processes are a circle of tree life which must be understood – or at the least appreciated – for its intricate and interconnected way of using what the environment makes available. A tree concentrates materials away from equilibrium and so lives. Tree health care providers are responsible for this large light driven engine, and for assuring benefits accrue and no harm befalls.

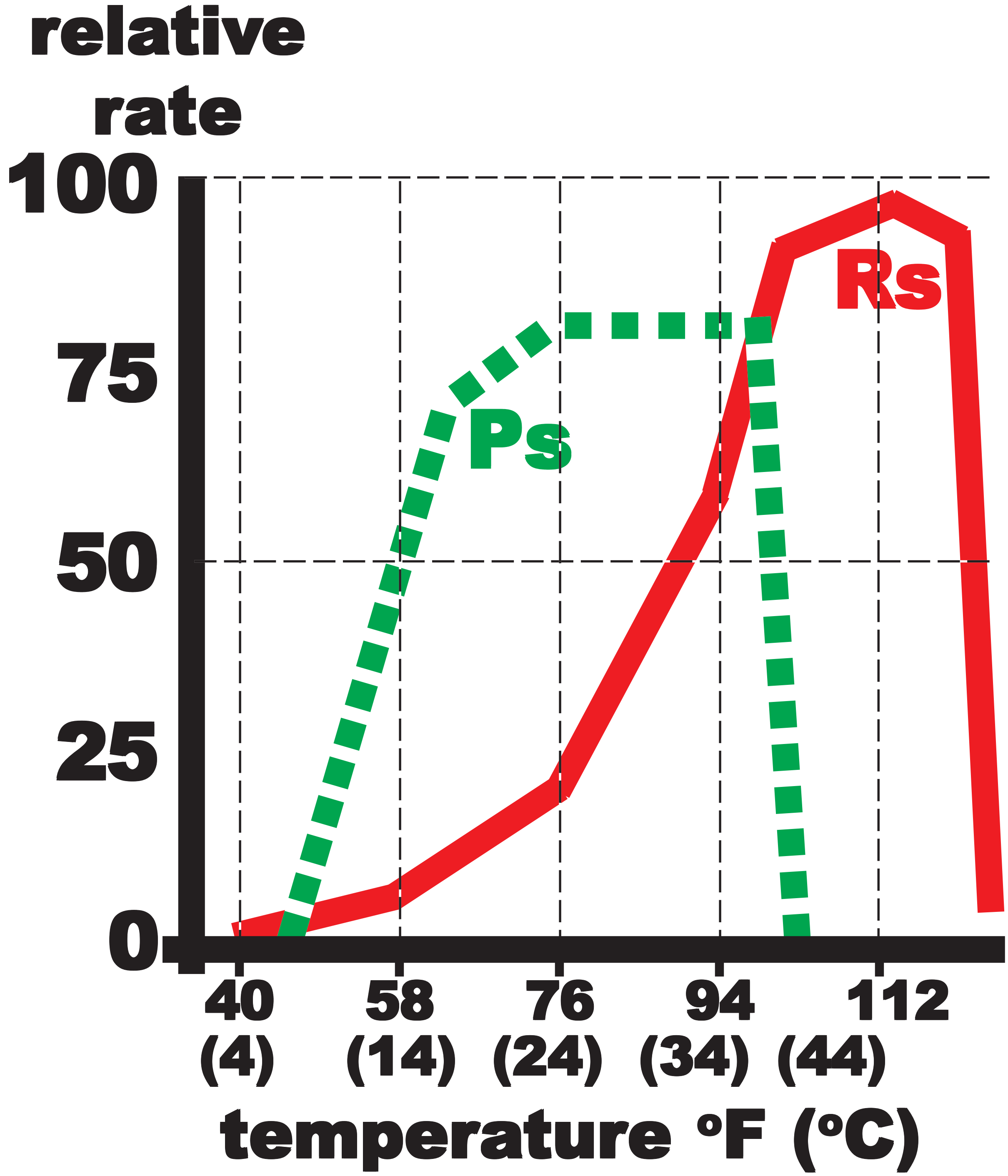

Figure 29: The relative rate of photosynthesis (Ps) and respiration (Rs) in a tree. Note respiration continues to climb exponentially with increasing temperatures and the photosynthesis process quickly falls apart as 105°F (41°C) is passed.

temperature °F (°C)	multiplier effect
40°F (4°C)	1X
58°F (14°C)	2X
76°F (24°C)	4X
94°F (34°C)	8X
112°F (44°C)	16X

Figure 30: Respiration doubling sequence for trees exposed to increasing heat loads. For each 18°F (10°C) site temperature increase above 40°F (4°C), respiration doubles due to physical and biological impacts of temperature.

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