The red maple paradox
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The Red Maple Paradox

What explains the widespread expansion of red maple in eastern forests?

Marc D. Abrams

One of the most dramatic changes that has occurred in forests of eastern North America during the twentieth century is the increase in the dominance of red maple (*Acer rubrum* L.; Lorimer 1984, Abrams 1992). Red maple has become nearly ubiquitous across sites of widely varying light, moisture, and nutrient availability. This distribution is in stark contrast to the limited distribution of red maple reported in pre-European settlement forests, where it occurred mainly in poorly drained areas. Red maple has increased after a wide range of disturbances and as a late successional species in many forest types. It now dominates the understory and mid-canopy of many oak (*Quercus*), pine (*Pinus*), and northern hardwood forests; moreover, it will probably continue to increase in dominance in the overstory during the next century, causing widespread replacement of the historically dominant trees of the forests of the eastern United States.

Surprisingly, red maple exhibits rather modest levels of leaf physiological responses (e.g., gas exchange and osmotic adjustment) to various environmental conditions and has leaf structural characteristics and nitrogen levels that are not particularly conducive to a robust leaf physiology. Therefore, the widespread expansion of red maple is a paradox in that it is not easily explained by its leaf physiology.

This "super-generalist" has low resource requirements and does many things reasonably well in a wide variety of ecological conditions

What morphological, physiological, and growth characteristics of red maple have facilitated its dramatic increase during the twentieth century? In this article, I attempt to resolve the red maple paradox by outlining the historical development and the present overstory and understory composition of forests with increasing red maple dominance, discussing major land-use and environmental changes that have occurred during the twentieth century, and relating red maple's ecophysiology and growth characteristics to these environmental changes. It appears that red maple has low resource requirements and is a "super-generalist" that has characteristics of both early and late successional species.

Pre-European distribution

Data from early land survey records indicate that before European settlement, red maple was a relatively minor component of most forests in the eastern United States (Table 1). For example, red maple represented less than 5% of surveyed trees in the northern hardwood–white pine–hemlock forests of Michigan and Wisconsin (Nowacki et al. 1990, Palik and Pregitzer 1992, Whitney 1994). Swamp forests in Michigan were dominated by larch (*Larix*), cedar (*Thuja*), and spruce (*Picea*), with only an occasional red maple (Whitney 1994). In the presettlement forests of southern Illinois, red maple was not recorded on upland sites but made up 4% of the trees on streambed terraces (Fralish et al. 1991). Red maple represented 3–6% of the trees on various soil types in northeastern Ohio, compared with 35–40% for beech (*Fagus grandifolia*) and white oak (*Quercus alba*; Whitney 1994).

Similarly, red maple was a minor component of the original forests of New England, which were dominated by beech, sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), spruce, and fir (*Abies*) in the north and by oak and pine in the south (Table 1; Siccama 1971, Lorimer 1977, Whitney 1994). In the Catskill Mountains of southeastern New York, red maple accounted for only 1% of the trees in the forests, which were dominated by beech, hemlock (*Tsuga canadensis*), and sugar maple (McIntosh 1962). In western New York, red maple was a minor component of the till plains and Allegheny Mountains (Seischab 1990).

By contrast to other forested regions of the eastern United States,

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Table 1. Pre-European settlement forest types within the current range of *Acer rubrum* in the eastern United States.

Dominant tree species	State	Reference
Lake States		
Tsuga, Fagus, Pinus strobus	MI	Palik and Pregitzer 1992
Pinus resinosa, Pinus banksiana, P. strobus	MI	Palik and Pregitzer 1992
Larix, Thuja, Picea	MI	Whitney 1994
Tsuga, Betula, Acer saccharum	WI	Nowacki et al. 1990
Pinus, Quercus, Populus	WI	Nowacki et al. 1990
New England		
Quercus alba, Quercus velutina, Pinus	MA	Whitney 1994
Picea, Fagus, Abies, Thuja, Betula	ME	Lorimer 1977
Fagus, A. saccharum, Picea, Betula, Tsuga	VT	Siccama 1971
Mid-Atlantic		
Fagus, Tsuga	PA	Abrams and Ruffner 1995
Pinus, Acer rubrum, Quercus, Castanea	PA	Abrams and Ruffner 1995
Quercus prinus, Q. alba, Pinus rigida, Castanea dentata	PA	Nowacki and Abrams 1992
Q. alba, P. strobus, Carya	PA	Nowacki and Abrams 1992
Q. alba, Quercus rubra	VA	Orwig and Abrams 1994
Quercus, Pinus, A. rubrum, A. saccharum	WV	Abrams and McCay 1996
Acer, Fagus, Betula, Pinus	WV	Abrams and McCay 1996
Fagus, Tsuga, A. saccharum, Betula	NY	McIntosh 1962
Fagus, A. saccharum, Tilia, Q. alba	NY	Seischab 1990
Southeast		
Fagus, Quercus, Magnolia	GA	Quarterman and Keever 1962
Pinus palustris, Pinus elliottii	FL	Braun 1950
Quercus, Carya, Pinus	GA	Nelson 1957
Quercus, A. rubrum, Liquidamber	GA	Nelson 1957
Midwest		
Fagus, A. saccharum, Q. alba	OH	Whitney 1994
Q. alba, Carya	OH	Whitney 1994
Q. alba, Q. velutina, Carya	OH	Whitney 1994
Quercus stellata, Carya	IL	Fralish et al. 1991
Q. alba, Q. velutina	IL	Fralish et al. 1991
Q. alba, Fraxinus americana, Fagus	IL	Fralish et al. 1991

red maple was an important component of some, but not all, forests in the mid-Atlantic region (Table 1). Red maple represented 20% of the trees on north-facing coves and stream valley sites in the Allegheny Mountains of central Pennsylvania (Abrams and Ruffner 1995). Moreover, it accounted for 12% of the trees in the Allegheny Mountains and 5–6% of those in the Ridge and Valley of eastern West Virginia (Abrams and McCay 1996), although it represented only 1% of the trees of northern Virginia's Piedmont and Coastal Plain (Orwig and Abrams 1994). In Georgia, red maple was reported frequently in bottomlands and, occasionally, in the dry uplands, which were dominated by oak, hickory (*Carya*), and pine (Nelson 1957).

Present-day distribution

Dramatic increases in red maple number and size have occurred in eastern forests during the twentieth century. In one of the first studies of these increases, Larsen (1959) reported on the invasion by red maple of oak forests in southern Wisconsin. Similarly, Lorimer (1984) documented an increase in red maple in the upland oak forests in Massachusetts and New York, and he suggested a future trend of increasing dominance for this species. Moreover, since 1880 one of the distinctive changes in the northern hardwood forests of the Catskill and Allegheny Mountains has been the increase in red maple (McIntosh 1962, Abrams and Ruffner 1995). In the Ridge and Valley of central Pennsylvania, a similar increase in red maple dominance has been reported for mixed-oak forests (Nowacki and Abrams 1992).

Presettlement northern hardwood–conifer and pine forests on dry–mesic sites in Wisconsin and Michigan that converted to red oak or aspen stands following early logging now have a greatly increased red maple component (Nowacki et al. 1990, Palik and Pregitzer 1992). From 1951–1993, red maple density increased over sixfold (from 191 stems of more than 2.5 cm per hectare to 1218 stems of that size) and basal area increased nearly sevenfold (from 0.52 to 3.55 m^2 per hectare) in an oak–hickory forest in North Carolina (Christensen 1977; Robert K. Peet, University of North Carolina, personal communication). In the subcanopy of a mature pine–oak forest in southern Arkansas, red maple density increased by more than 300% between 1954 and 1992 (Cain and Shelton 1995). An acceleration of red maple dominance to 70% of the present overstory-importance value occurred after logging of mature oak forests in the 1930s in central Pennsylvania (Abrams and Nowacki 1992).

As a result of these increases, red maple has become one of the most abundant and widespread tree species in the eastern United States. Its range is bounded by Maine, Minnesota, eastern Texas, and Florida, excluding the Prairie Peninsula in the north–central Plains (Burns and Honkala 1990). Throughout its range, red maple thrives on many landforms, in many different soil conditions, and under widely varying moisture and light regimes. In fact, red maple occurs on landforms as different as dry ridges and swamps, on soil textures varying from sands to clays, on soils with pH ranging from highly acidic to near neutral, and from high-light to deeply shaded sites.

In the Big Thicket forests of eastern Texas, for example, red maple occupies sites varying from upper slope pine–oak forests to swamp cypress (*Taxodium*)–tupelo (*Nyssa*; Marks and Harcombe 1981). In central Massachusetts, red maple is one of the most abundant tree species on sites ranging from sand plains to ridge crests and cove forests (Whitney 1994). In central Pennsylvania and eastern West Virginia, red maple is now a principal species on all major landforms and physiographic units in the Allegheny Plateau and Mountains and in the Ridge and Valley (Abrams and Nowacki 1992, Abrams and Ruffner 1995, Abrams and McCay 1996). Red maple is characteristic of most forest types in Maryland, ranging from poorly drained to dry, although it is not the primary dominant tree species in any of them (Brush et al. 1980). In Alabama, red maple occurs in most forest sites, ranging from swamp to upland bluff, but it dominates mesic floodplains and stream-bottom communities (Golden 1979).

The dominance of red maple in forests is not equivalent across all landforms and soil types. In particular, sugar maple may outcompete red maple on mesic, nutrient-rich sites in many regions. For example, whereas dry oak forests in Michigan are exhibiting a succession to red maple domination, mesic sites, with more rapid nitrogen turnover, are dominated by sugar maple (Host et al. 1987). In Wisconsin, red oak stands on mesic, silt–loam soils are converting to sugar maple forests, whereas dry–mesic, loamy sand soils are converting to red maple forests (Nowacki et al. 1990). In Massachusetts, red maple shows the highest affinity for dry mid-slopes, whereas sugar maple prefers mesic lower slope and cove forests (Whitney 1994).

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Q. alba, Fraxinus americana, Fagus	IL	Fralish et al. 1991

Figure 1. High density of pole-sized red maple (*Acer rubrum*) in a mature mixed-oak (*Quercus*) forest in central Pennsylvania in which fire has been suppressed during the twentieth century.

The competition between the two maple species often results in a bimodal distribution for red maple within a region, with red maple occupying the wet and dry sites and sugar maple occupying the mesic sites. However, sugar maple is also an important climax species replacing oak in forests in the Prairie Peninsula region of Illinois and Missouri, which is outside of the red maple's range (Adams and Andersen 1980, Pallardy et al. 1988). Despite the relatively dry climate of the Prairie Peninsula, the abundance of nutrient-rich Mollisol and Alfisol soils is apparently more conducive to domination by sugar maple than red maple. Conversely, the range of red maple includes the entire southeastern Coastal Plain and Piedmont (from eastern Texas and Arkansas to northeastern Virginia), which includes an abundance of nutrient-poor Ultisol soils, in which sugar maple does not occur. Therefore, sugar maple distribution in the southern United States is seemingly limited by a lower tolerance than red maple of warm temperatures and nutrient-poor, acidic sites.

Impacts of land-use and environmental changes

Much of the increase in red maple, particularly in upland oak and pine forests, may be a result of fire suppression during the twentieth century (Lorimer 1984, Abrams 1992). Red maple is more sensitive to fire than many other forest trees; periodic burning associated with the activities of Native Americans, lightning strikes, and logging and mining by European settlers presumably kept red maple populations in check prior to 1900. Indeed, a single understory burn in an oak forest in Wisconsin killed 70% of the red maple seedlings (Reich et al. 1990). The deliberate suppression of forest fire during this century has, consequently, allowed for the increase of red maple in many eastern forests as a later successional species (Figure 1).

The expansion of red maple may also be related to its opportunistic establishment and growth following a variety of disturbances, such as logging, land clearing, agricultural abandonment, wind throw, and insect and disease outbreaks (e.g., gypsy moth and chestnut blight; Golden 1979, Burns and Honkala 1990, Abrams and Nowacki 1992, Fajvan and Wood 1996). The unique ability of red maple to behave as both an early and a late successional species and to thrive in widely varying edaphic conditions has therefore promoted its increase in both disturbed and fire-suppressed landscapes.

Along with fire exclusion, many eastern forests have also experienced a dramatic increase in white-tailed deer (*Odocoileus virginianus*) populations during the twentieth century. Because oak foliage and acorns are a highly preferred food for these deer, intensive browsing may have contributed significantly to a decline in oak regeneration (Bramble and Goddard 1953). Indeed, oak acorns may represent 76% by volume of the deer's diet during years of abundant acorn protection (Harlow et al. 1975). However, deer also browse heavily on red maple (and sugar maple) twigs, and small mammals eat large amounts of maple seed, as well as oak acorns. After a northern hardwood forest was clear-cut, red maple produced most of the new twigs as a result of vigorous stump sprouting (Hughes and Fahey 1991). By the third year after logging, the total removal of twigs by deer (mainly in winter) was highest for red maple among the four preferred browse species. Consistent with these results, red maple declined 50–90% in the smallest diameter classes between 1929 and 1978 in a northern hardwood–conifer forest in northern Pennsylvania as a result of heavy deer browsing (Whitney 1984). However, deer avoided browsing on red maple, preferring hemlock and black

Table 2. Leaf physiological responses of various eastern hardwood species in shaded understory or greenhouse conditions in eastern North America.

Species	A_{max}[a,b]	R[c]	K[d]	LCP[e]	Reference
Aesculus glabra	3.3	0.3	200	22	Bazzaz and Carlson 1982
Acer rubrum	3.6	0.5	139	22	Kloeppel et al. 1993
A. rubrum	2.6	0.4	168	12	Loach 1967
A. rubrum	4.4	0.2	120	—[f]	Jurik et al. 1988
A. rubrum	2.7	0.4	117	20	Kubiske and Pregitzer 1996
Acer saccharum	3.9	0.1	115	—	Jurik et al. 1988
A. saccharum	3.4	0.4	83	13	Bazzaz and Carlson 1982
Betula papyrifera	4.0	0.7	85	16	Kubiske and Pregitzer 1996
Fagus americana	9.7	0.1	200	1	Bazzaz and Carlson 1982
Fagus grandifolia	4.3	0.9	301	11	Loach 1967
F. grandifolia	5.2	0.3	575	8	Teskey and Shrestha 1985
F. grandifolia	4.4	0.1	115	—	Jurik et al. 1988
Liquidamber styraciflua	5.1	0.8	525	8	Teskey and Shrestha 1985
Liriodendron tulipifera	6.6	1.5	301	26	Loach 1967
L. tulipifera	7.7	1.2	720	15	Teskey and Shrestha 1985
Platanus occidentalis	7.0	0.2	175	5	Bazzaz and Carlson 1982
Populus tremoloides	8.8	3.5	880	43	Loach 1967
Prunus pennsylvanica	5.0	0.4	126	15	Bazzaz and Carlson 1982
Prunus serotina	3.7	0.1	115	—	Jurik et al. 1988
Quercus alba	6.6	0.7	650	6	Teskey and Shrestha 1985
Quercus imbricaria	4.7	0.3	497	28	Bazzaz and Carlson 1982
Quercus prinus	4.8	0.9	152	33	Kloeppel et al. 1993
Quercus rubra	4.5	0.5	250	11	Loach 1967
Q. rubra	7.0	0.8	700	21	Teskey and Shrestha 1985
Q. rubra	4.7	0.1	115	—	Jurik et al. 1988
Q. rubra	2.4	0.4	121	24	Kubiske and Pregitzer 1996
Q. rubra	7.4	0.2	200	5	Bazzaz and Carlson 1982
Quercus velutina	6.3	0.5	361	29	Kloeppel et al. 1993
Tilia americana	4.8	0.1	135	—	Jurik et al. 1988
T. americana	3.3	0.2	130	20	Bazzaz and Carlson 1982
Sassafras albidum	7.6	0.3	561	22	Kloeppel et al. 1993

[a] Maximum net photosynthesis.
[b] All units are in μmol · m^{-2} · s^{-1}.
[c] Dark respiration.
[d] Light saturation constant.
[e] Light compensation point.
[f] Data not available.

birch (*Betula lenta*), in a mixed-species forest in southern New England (Kittredge and Ashton 1995).

Although these data suggest that deer browsing has affected red maple during this century, its impact on oaks may have been more severe. This differential effect has been exacerbated by the fact that oak has less frequent mast years than red maple. Moreover, oak may be a more highly preferred browse species than red maple during the summer, and summer browsing has a much greater impact on subsequent tree growth and survival than winter browsing (Bramble and Goddard 1953; Kurt W. Gottschalk, US Forest Service, Morgantown, WV, personal communication). Consequently, the increase in red maple and decrease in oak in eastern forests during the twentieth century may be explained, in part, not only by forest fire suppression and landscape disturbance, but also by the differential impacts of deer.

Differential defoliation by the gypsy moth may also be involved with the increase in red maple and decrease in oaks in eastern forests during the twentieth century. Gypsy moth prefer oak to red maple because of the presence of alkaloid chemicals in red maple foliage (Barbosa and Krischik 1987). The concentration of gypsy moth defoliation of overstory oaks has benefitted red maple during the twentieth century (Fajvan and Woods 1996). The alkaloids in red maple foliage may also deter summer browsing by deer (Jack C. Schultz, Pennsylvania State University, personal communication).

The dramatic increase in atmospheric carbon dioxide levels during the twentieth century may have had a significant impact on the ecology and physiology of red maple and other tree species. However, although red maple responds to elevated carbon dioxide with increased photosynthetic performance and biomass production, these responses are not necessarily greater than those of other, co-occurring tree species (Bazzaz et al. 1993, Kubiske and Pregitzer 1996). Indeed, the relative increase in red maple biomass in response to elevated carbon dioxide was intermediate among five tree species studied (Bazzaz et al. 1993). Moreover, red oak exhibited a much greater increase in total net photosynthesis than red maple in response to elevated carbon dioxide in both sun and shade (Kubiske and Pregitzer 1996). Elevated carbon dioxide increased the net root production in paper birch (*Betula papyrifera*) but not red maple (Berntson and Bazzaz 1996). These results suggest that the large increase of red maple compared with other tree species is unlikely to be directly related to the elevated levels of atmospheric carbon dioxide this century. Whether red maple has increased in response to global warming or to the effects of acid rain in the twentieth century is unknown.

Leaf physiology, morphology, and nitrogen

The nearly ubiquitous increase in red maple in the understory of many forest types suggests some unique physiological attributes for this species in shaded environments. However, leaf-level physiological studies do not provide clear evidence for red maple's competitive superiority over other tree species in shade.

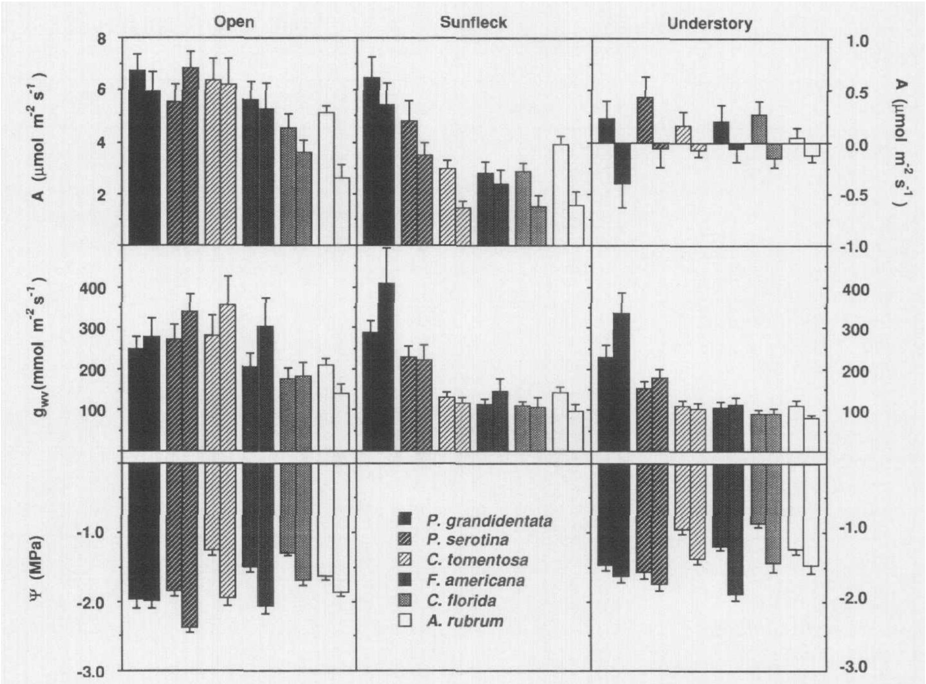

Figure 2. Leaf physiological responses for six tree species (bigtooth aspen [*Populus grandidentata*], black cherry [*Prunus serotina*], mockernut hickory [*Carya tomentosa*], white ash [*Fraxinus americana*], flowering dogwood [*Cornus florida*], and red maple [*Acer rubrum*]) in 1993 on a mesic valley floor site in central Pennsylvania. Measurements were made under both well-watered (left bar of each pair) and drought (right bar of each pair) conditions. Three physiological parameters were measured: mean (+ SE) midday net photosynthesis (A), leaf conductance to water vapor diffusion (gwv), and leaf water potential (Ψ). All parameters were measured in open, sunfleck, and shaded understory leaves, except for leaf water potential, which was not measured in sunfleck leaves. The scale for the graph of A in understory leaves is different from that used for open and sunfleck leaves; all other graphs use the same scale for all sets of leaves. Adapted from Abrams and Mostoller (1995).

Leaf physiology. Red maple is typically rated as shade tolerant, and it has a relatively low rate of net photosynthesis (A) in shade, even though its respiration rate, light saturation constant (i.e., the amount of light needed to approach maximum rates of photosynthesis), and light compensation point (i.e., light intensity when A = 0) are lower than those of earlier successional trees (Table 2). However, in an oak forest understory in Wisconsin, the photosynthetic rate of shaded leaves of red maple was similar to those of black cherry (*Prunus serotina*) and northern pin oak (*Quercus ellipsoidalis*; Reich et al. 1990). Red maple has also been reported to have higher area-based photosynthesis and higher diurnal shoot-level assimilation than sugar maple (Sipe and Bazzaz 1994). The finding that red maple has lower net photosynthesis in shade than earlier successional hardwoods may, however, be somewhat misleading because of the short duration of most field and greenhouse physiology studies. Physiological measurements repeated on the same seedling or sapling over many years in the same level of shade may ultimately show higher total net photosynthesis in red maple, because species with lower shade tolerance will show more pronounced aging effects during prolonged understory suppression.

The intrinsically low photosynthetic rate of red maple relative to earlier successional hardwoods is also seen in high-light environments (Jurik 1986, Reich et al. 1990, Kloeppel et al. 1993, Kubiske and Abrams 1994, Kubiske and Pregitzer 1996). In a study of leaf gas exchange and water potential of six hardwood species on a mesic valley site in central Pennsylvania, red maple had significantly lower net photosynthesis and leaf conductance of water vapor (gwv) than two earlier successional species, bigtooth aspen (*Populus grandidentata*) and black cherry, in both open-growing plants and understory plants in shade and sunflecks (Figure 2; Abrams and Mostoller 1995). These differences existed in both nondrought and drought conditions; red maple exhibited the largest percentage decrease in photosynthetic rate during drought of all six study species in both open and sunfleck environments. However, before the drought, the red maple leaves that were measured in understory sunflecks had higher net photosynthesis than those of three of the other study species, including mockernut hickory (*Carya tomentosa*) and white ash (*Fraxinus americana*), both of which are considered to be mid-successional species. This last finding suggests that red maple may better utilize sunflecks for carbon gain than some earlier successional and late successional tree species during nondrought conditions.

Red maple maintained relatively low, but similar, levels of photosynthesis in both wet and dry years on a xeric ridge in Pennsylvania (Kubiske and Abrams 1994). After an oak forest understory was burned, net photosynthesis for black cherry and oak seedlings was enhanced compared with the unburned control, but that of red maple was not, indicating that the physiology of red maple is more sensitive to fire than other hardwoods (Reich et al. 1990).

Red maple has near average osmotic potential values among North American tree species (Abrams 1988). However, this species typically has very limited osmotic adjustment (i.e., accumulation in plant tissues of solutes such as sugars, amino acids, and salts) during drought (Roberts et al. 1980, Abrams and Kubiske 1990b, Kubiske and Abrams 1994). Therefore, it is un-

Table 3. Mean foliar nitrogen content (g/m² and %) for broad-leaved tree species in various light regimes in situ in eastern North America.

Species	Light regime	State	N (g/m²)	N (%)	Reference
Acer rubrum	Gap	WI	0.85	1.73	Reich et al. 1990
A. rubrum	Open	WI	1.25	1.80	Reich et al. 1991
A. rubrum	Open	PA	1.09	1.58	Abrams and Mostoller 1995
A. rubrum	Understory	PA	0.60	1.51	Abrams and Mostoller 1995
A. rubrum	Sun	MI	0.61	1.14	Kubiske and Pregitzer 1996
A. rubrum	Shade	MI	0.57	2.20	Kubiske and Pregitzer 1996
Acer saccharum	Open	WI	1.20	2.00	Reich et al. 1991
Betula papyrifera	Sun	MI	1.98	2.62	Kubiske and Pregitzer 1996
B. papyrifera	Shade	MI	0.88	2.93	Kubiske and Pregitzer 1996
Carya tomentosa	Open	PA	1.93	2.25	Abrams and Mostoller 1995
C. tomentosa	Understory	PA	0.81	2.05	Abrams and Mostoller 1995
Cornus florida	Open	PA	1.04	1.50	Abrams and Mostoller 1995
C. florida	Understory	PA	0.56	1.76	Abrams and Mostoller 1995
Fraxinus americana	Open	PA	1.59	1.76	Abrams and Mostoller 1995
F. americana	Understory	PA	0.57	1.71	Abrams and Mostoller 1995
Populus grandidentata	Open	PA	1.70	2.24	Abrams and Mostoller 1995
P. grandidentata	Understory	PA	1.25	2.24	Abrams and Mostoller 1995
Prunus serotina	Gap	WI	1.03	2.44	Reich et al. 1990
P. serotina	Open	PA	1.55	1.84	Abrams and Mostoller 1995
P. serotina	Understory	PA	0.87	2.10	Abrams and Mostoller 1995
Quercus ellipsoidalis	Gap	WI	1.16	2.09	Reich et al. 1990
Q. ellipsoidalis	Open	WI	2.10	2.10	Reich et al. 1991
Quercus rubra	Sun	MI	2.11	1.98	Kubiske and Pregitzer 1996
Q. rubra	Shade	MI	0.96	2.61	Kubiske and Pregitzer 1996

likely that an ability to osmotically adjust explains red maple's ability to grow on drought-prone sites; instead, perhaps red maple conserves moisture through effective stomatal control.

Leaf morphology and nitrogen. The structure of leaves can be significantly related to their physiological function (Abrams et al. 1994). When comparing sun and shade leaves of tree species within the same study area, red maple leaves of both types tend to have low to average values for leaf area, thickness, mass per area, stomatal density, and guard cell length (Abrams and Kubiske 1990a, Kloeppel et al. 1993, Abrams and Mostoller 1995). Higher gas-exchange rates are typically linked to increases in these leaf structural parameters (Jurik 1986, Reich et al. 1991, Abrams et al. 1994). The small guard cells of red maple leaves may, however, be an adaptation to help control water loss in xeric or high-light environments (Abrams and Kubiske 1990a). Red maple leaves also display significant plasticity to sun and shade environments and exhibit genotypic variation in structure between bottomland and upland populations (Abrams and Kubiske 1990a, 1990b). Thus, although the leaf morphology of red maple appears not to be conducive to high rates of gas exchange, it is functional in a variety of site and climatic conditions.

In most plant species, low leaf nitrogen is related to low photosynthetic performance (Reich et al. 1991). Foliar nitrogen levels in red maple are usually below those of other tree species on the same or different sites, including open, gap, or understory environments (Table 3). Higher nitrogen content in leaves of open-growing red maple and other tree species is due to increased leaf thickness and mass per area compared with leaves of understory plants. Red maple typically has low photosynthetic nitrogen-use efficiency in high light relative to other hardwood species (Reich et al. 1990, Abrams and Mostoller 1995, Kubiske and Pregitzer 1996). Red maple foliage also has lower percentages of phosphorus and potassium than black cherry and northern pin oak in burned and unburned forest understories, particularly during the early and middle growing season (Reich et al. 1990). Therefore, the low net photosynthesis in red maple is probably a consequence of its modest leaf structural characteristics and low nutrient levels. These leaf morphological and chemical features are consistent with those of other late successional tree species (Abrams and Kubiske 1990a, Reich et al. 1991, Abrams and Mostoller 1995).

Seed phenology, growth, and biomass distribution

The findings discussed above suggest that the dramatic increase in red maple dominance cannot be easily explained by its leaf physiology, morphology, or chemistry. Therefore, the ecology of red maple may be better understood by evaluating aspects of its vegetative and reproductive growth and demography. Can red maple seed phenology, above- and belowground growth, biomass distribution, or tree mortality rates under varying environmental conditions more fully explain the red maple paradox?

Seed phenology. The seed phenology of red maple, in which seeds are produced, disseminated, and germinate in the spring and early summer, is unique among upland hardwoods of the eastern United States; this seed phenology is more typical of riparian and floodplain tree species (Burns and Honkala 1990). Requirements for red maple seed germination are not stringent, and most seeds germinate soon after dissemination. However, seeds that fall under a dense overstory canopy may not germinate until the second year after they are produced. In addition, seeds from some northern populations of red maple have a prechilling requirement;

these seeds also do not germinate until the second year.

By contrast to red maple, most upland hardwoods disseminate seeds in the fall that germinate the following spring or, in the case of white oaks, the same fall in which they matured. With few exceptions, red maple seeds or newly germinated seedlings do not overwinter before their first summer growing season, which prevents potentially large winter losses of the type experienced by many other tree species. However, seeds and seedlings of other tree species that survive the winter may germinate or undergo spring growth earlier than the new seeds of red maple, resulting in a longer growing season. Therefore, both red maple and other upland hardwoods have potential competitive advantages and disadvantages in their seed ecology. Nevertheless, the fact that many forests have many more seedlings of red maple than of other tree species indicates that red maple's unique seed phenology, combined with its early sexual maturity (e.g., 4–10 years), prolific seed production, and high shade tolerance, contibutes to its success (Lorimer 1984, Nowacki et al. 1990, Abrams and Nowacki 1992).

Table 4. Physiological and ecological attributes of red maple relative to other hardwood tree species in eastern North America.

Attribute	Relative level
Geographic range	High
Ecological breadth	High
Genetic variation	High
Acclimation potential	High
Longevity	Average–high
Early sexual maturity	High
Seed production	Average–high
Frequency of mast years	High
Understory tolerance	High
Fire resistance	Low
Deer browse	Average
Gypsy moth defoliation	Low
Shoot growth—low light	Low
Shoot growth—high light	Average–high
Sprouting ability	High
Rooting depth	Low–average
Nutrient requirements	Low
Leaf nitrogen content	Low
Leaf xeromorphism	Low
Net photosynthesis	Low
Photosynthetic nitrogen use efficiency	Low
Transpiration	Low
Respiration	Low
Light compensation point	Low
Drought impacts on gas exchange	Low–average
Osmotic potentials	Average
Osmotic adjustment	Low
Carbon dioxide impacts on gas exchange	Low
Carbon dioxide impacts on growth	Low–average

Growth and biomass distribution. Red maple typically has lower shoot and root growth in shade than other tree species in greenhouse experiments, although this difference may not reflect the situation in the field (see below). For example, whereas one-year-old red maple seedlings in 2% full sunlight in combinations of high and low water and high and low nitrogen had a shoot biomass of approximately 25 mg, red oak seedlings had shoot biomass values of 650–800 mg (Canham et al. 1996). Even in higher light, red maple shoots grow more slowly than red oak shoots, particularly in the low-nitrogen and low-water treatments. In low light, red maple root biomass was approximately 15–20% lower than that of red oak, but this difference disappeared at higher light levels (Canham et al. 1996). Red maple seedlings also grew more slowly than red oak and black cherry seedlings and, after two years, had a lower root-to-shoot ratio than black oak (*Quercus velutina*; Gottschalk 1985).

In contrast to these studies, however, the total above- and belowground biomass of red maple equaled or exceeded that of five other hardwood species in treatments of high and low light, nitrogen, and carbon dioxide (Bazzaz et al. 1993).

In the field, red maple seedlings grow faster in small and moderate-sized forest gaps than red oak, yellow birch, and hemlock; however, in large forest openings or gaps, red maple seedlings grow more slowly than red oak (Hibbs 1982). The height growth rate of red maple sprouts may equal that of the fast-growing bigtooth aspen in early succesional forests (Palik and Pregitzer 1993). In response to canopy gaps, red maple may be more architecturally plastic than sugar maple in branch number, leaf number, and total leaf area (Sipe and Bazzaz 1994). Red maple may also exhibit plasticity in root morphology on contrasting sites, such as swamps and dry uplands. In most red maple trees, the roots form in the upper 25 cm of soil, but the maximum rooting depth of mature red maple is 2–3 m (Burns and Honkala 1990). This rooting depth is typical of many eastern hardwoods, excluding the more deeply rooted trees, such as oaks (Stone and Kalisz 1991). However, the lower allocation of carbon to root mass in red maple than in upland oaks may help to explain why red maple trees grow faster than oaks in forest understories in the absence of periodic burning.

Red maple tree mortality. Mortality rates may provide important clues to the long-term dynamics and survival of forest trees. In a 19-year study in Massachusetts of nine tree species in the understory, red maple, sugar maple, and pignut hickory had the highest survival rate (70–83%), and white ash, red oak, and paper birch the lowest survival rate (2–11%), leading to a high shade tolerance rating in the former group of tree species and a low tolerance rating in the latter (Lorimer 1983). Moreover, red maple trees had lower drought-induced mortality than oaks and other mixed-hardwood species (Elliott and Swank 1994). The predicted mortality rate for red maple saplings growing under beech, hemlock, and sugar maple was relatively high, but lower than that predicted for red oak and white ash (Canham et al. 1994).

Conclusions

Among eastern North American tree species, red maple is one of the most broadly distributed: It can thrive on a variety of sites, including successional communities ranging from pioneer to subclimax or climax. The suite of ecophysiological characteristics for red maple indicates that no single trait can adequately explain the dramatic expansion of red maple to its broad current distribution. Instead, red maple seems to do many things reasonably well in a wide variety of habitats and ecological conditions. This ability may be best explained by the facts that red maple possesses physiological, morphological, and growth characteristics of both early and late successional tree species and that it requires less water, nutrients, and light for survival than many other tree species in the eastern United States (Table 4).

The maximum longevity of red maple can exceed 200 years, which is above average for many eastern hardwoods but less than the 300–400-year lifespan of the longest-lived trees, such as white oak, sugar maple, and beech. Red maple reaches sexual maturity at a young age, produces large numbers of seeds with few germination requirements, and disperses them readily (Burns and Honkala 1990). These reproductive traits are characteristic of many early successional trees, and when combined with spring seed phenology and vigorous sprouting, they allow for the development of large numbers of seedlings and sprouts. Red maple exhibits high genetic diversity in many physiological and growth characteristics, including cold hardiness, time of seed germination, time and degree of flushing, time of budset, growth rate, stem form, fall coloration, and ecotypic variation in drought tolerance and leaf morphology (Townsend and Roberts 1973, Abrams and Kubiske 1990b, Burns and Honkala 1990). Red maple has several varieties, or taxa, including trilobum and drummondii, and distinct forms based on leaf and branch morphology, including pallidiflorum, tomentosum, and breviramusculum (Fernald 1987). Natural hybridization also occurs between red maple and silver maple (*Acer saccharinum*). The high genetic diversity, including the ability to hybridize and establish distinct genotypes, has contributed to the widespread ecological success of the species on contrasting sites.

Despite relatively low photosynthetic rates in shade, red maple exhibits high understory tolerance, which may be explained by its low respiration rate, light compensation point, and light saturation constant (Table 4). With adequate light, net photosynthesis in red maple can exceed that of other late successional tree species and may even approach that of mid-successional trees (Figure 2). Moreover, red maple sprouts can grow quickly in high light. Red maple has high survival rates on drought-prone sites, but it has relatively low leaf xeromorphism, limited osmotic adjustment, limited rooting depth, and high stomatal and mesophyll limitation to photosynthesis during drought. Therefore, red maple's success on dry sites may be related to its ability to avoid desiccation by more effective stomatal control of water loss than tree species with intrinsically high transpiration rates (Kloeppel et al. 1993). Finally, red maple has an indeterminate growth habit, and it may halt shoot growth during the peak drought period and resume growth when the drought has ended (Burns and Honkala 1990). These physiological and growth responses may result in the relatively low mortality of red maple trees subjected to prolonged understory suppression or periodic drought. Moreover, red maple's ability to grow on low-nutrient sites may be related to its low foliar nutrient requirements.

The complex physiology of seed production, vegetative growth, and shade tolerance of plants, including red maple, cannot be adequately explained by leaf-level physiology. Indeed, the ecology of many species may be more related to plant architecture, carbon and biomass allocation, growth potential, seed dispersal, seedling establishment, herbivore impacts, and mortality rates than to their rates of photosynthesis (Walters et al. 1993). Field studies of annual height growth or radial growth of tree rings, which integrate seasonal whole-plant physiology, indicate that red maple trees in the understory grow at average to above average rates and that their growth can be further enhanced following the opening of overstory gaps, even after decades of suppression (Hibbs 1982, Abrams and Downs 1990, Palik and Pregitzer 1993, Abrams et al. 1995). High shade tolerance allows red maple to persist in the forest understory, whereas its rapid growth responses to episodic light promotes gap capture and canopy ascension.

The two key ecological attributes of red maple are its ability to act as both an early and late successional species and to thrive on sites of greatly contrasting edaphic conditions. These traits, which are rare among plant species, have allowed red maple to increase in response to the wide range of land-use and environmental changes that followed European settlement. As an early successional species, red maple can be opportunistic following forest disturbances and agricultural abandonment. As a later successional species, red maple can increase in many forest types in which periodic fire has been suppressed. This species has also increased in many forests affected by deer and gypsy moth herbivory because it is less preferred than most other trees. In eastern forests, red maple has become the quintessential highly competitive "super-generalist" that seems to thrive in most edaphic situations and successional stages. Its physiology provides only a partial explanation for the red maple paradox. The adaptability of most organisms to widely varying environments is related to genotypic and phenotypic variation. A few studies have begun to address these characteristics of red maple, and future studies of root, shoot, and reproductive physiology and growth in response to environmental gradients of light, water, and nutrients should provide a better explanation of the red maple paradox.

Given the current ecology and management of eastern forests, the increasing dominance of forest overstories by red maple seems inevitable. The loss of oak and pine domination in eastern United States forests will be a primary consequence of continued red maple expansion. Periodic burning of oak and pine forests before European settlement was arguably a key factor limiting red maple domination in the original forests (Abrams 1992). The increased use of prescribed understory burning may be the most effective ecosystem management approach for keeping red maple populations in check and restoring the health and vigor of the historically dominant oak and pine forests.

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