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Regeneration of Red Oak (*Quercus rubra* L.) Using Shelterwood Systems: Ecophysiology, Silviculture and Management Recommendations

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Regeneration of Red Oak (*Quercus rubra* L.) Using Shelterwood Systems: Ecophysiology, Silviculture and Management Recommendations

by

Daniel C. Dey
William C. Parker

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Ontario Ministry of Natural Resources
Ontario Forest Research Institute
P.O. Box 969, 1235 Queen Street East
Sault Ste. Marie, Ontario
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Ministry of Natural Resources
Ontario Forest Research Institute
P.O. Box 969
1235 Queen Street East
Sault Ste. Marie, Ontario
P6A 5N5

Telephone: (705) 946-2981
Fax: (705) 946-2030
E-mail: ofriin@epo.gov.on.ca

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Abstract

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There is considerable interest in developing reliable methods for regenerating red oak (*Quercus rubra* L.) in Ontario. Traditional silvicultural methods have not been successful in maintaining the current levels of oak growing stock. In this paper, we review the ecology, physiology and reproductive biology of red oak. This discussion stresses the importance of seedling ecophysiology and regeneration ecology to the use and further development of the shelterwood method for regenerating red oak. Silvicultural recommendations based on the best information currently available are presented.

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1.0 Introduction

Red oak (*Quercus rubra* L.) is an important member of the Great Lakes-St. Lawrence and Deciduous forest regions of Ontario. The species exists at the northern limit of its native range in Ontario and occurs throughout the southern and central regions of the province. It also inhabits the area bordering the northern shore of Lake Huron and along the Minnesota-Ontario boundary (Figure 1).

In Ontario, red oak occurs on sites with a wide variety of soil types and topographic positions in Site Regions 4E, 5E, 6E and 7E (Hills 1959). It is most common on sites with normal to hot ecoclimates and dry to fresh moisture regimes.

Red oak commonly dominates the overstory on shallow-soiled, rocky ridges in the Central Region. On the drier, hotter sites, it grows in association with white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.). On more productive sites, it grows with sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), American basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* [L.] Carr.), and other northern hardwoods. Poplars (*Populus* spp.), white birch (*Betula papyrifera* Marsh.), black cherry (*Prunus serotina* Ehrh.) and other shade intolerant species grow with red oak where major stand disturbances such as fire and logging have occurred.

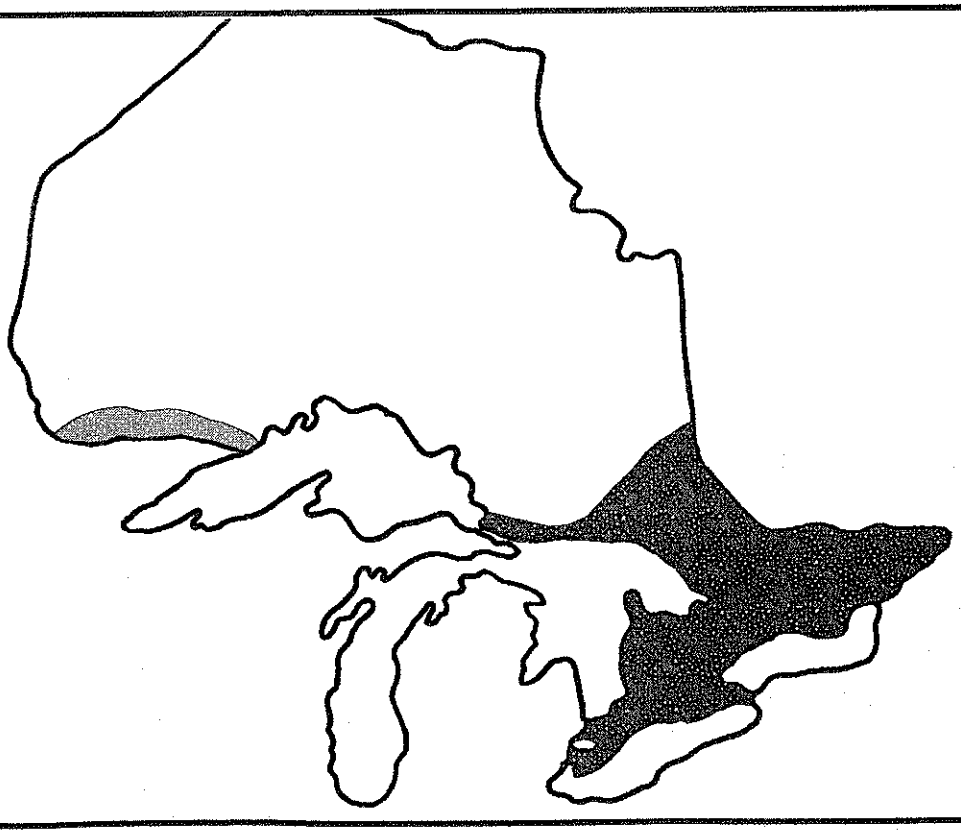

Figure 1. *The distribution of red oak in Ontario.*

Figure 2. *In Ontario, European settlers cleared and burned the forest for agricultural and subsistence purposes. Natural and anthropogenic fires burned uncontrolled over large areas. Organized fire suppression did not begin until the 1920s.*

Oaks have been a dominant component of hardwood and oak-pine-mixed hardwood forests of North America for several thousand years (Lorimer 1993). Land use practices or natural disturbances that reduced understory vegetation were the factors that most likely favored the establishment and maintenance of oak-dominated forests. Before European settlement, wildfire and burning of the forest understory by native North Americans promoted the recruitment of the more fire resistant oak species over less resistant, shade tolerant species. In the post-settlement era, European settlers maintained this practice of understory burning to create open woodlands for improved hunting and grazing conditions, and to clear the forest for other agricultural purposes (Figure 2) (Pyne 1982, Guyette and Dey 1995). Clearcut logging, often followed by burning of logging slash and grazing by livestock, also appears to have promoted oak regeneration during this period (Nowacki et al. 1990, Abrams 1992, Lorimer 1993).

In the 1930s, the advent of fire suppression and a growing interest in forest management and conservation resulted in a reduced frequency of these types of disturbances (Guyette and Dey 1995). Research addressing the historical development and displacement of oak from stands formerly dominated by these species also point to 1930 to 1940 as an ecological turning point after which oak regeneration failures became increasingly common (Lorimer 1993). In the absence of fire and other disturbances, oak forests have developed shade tolerant understories that dominate the growing space when gaps in the canopy occur (Coder et al. 1987; Perkey 1987; Dey, unpubl.).

In recent decades, researchers have found oak forests in Ontario and throughout eastern North America to be undergoing successional displacement by more shade tolerant species such as sugar maple (Crow 1988; Pallardy et al. 1988; Schlesinger 1989; Lorimer 1993; Dey, unpubl.). Traditional methods of selective harvesting, unfortunately, appear to be accelerating this succession (Schlesinger 1976, Smith 1980, Della-Bianca and Beck 1985, Heiligmann et al.

1985, Loftis 1985). Oak regeneration failure is a particularly serious problem in mesic habitats, where the potential growth and quality of red oak is greatest. Historical trends in many red oak stands in northern Wisconsin strongly suggest that a lack of heavy disturbance will result in continued replacement of the oak by shade tolerant species on all but the driest sites (Nowacki et al. 1990).

Several other factors are currently contributing to the loss of red oak from the forest landscape. Although the problem of oak regeneration is widespread, the causes are in some instances quite localized. Oak decline, insect defoliation (e.g., gypsy moth, *Lymantria dispar* L.) and deer browsing predispose oak to negative effects from other stresses such as water deficits. These factors decrease a tree's capacity to produce acorns and may increase the mortality rate of both seedlings and larger trees (Figure 3) (Wood 1938, Marquis et al. 1976, Hicks et al. 1993).

Figure 3. *Oak decline is a stress-insect-disease complex that causes growth reductions, crown dieback and mortality in red oak in Ontario. It is most prevalent in mature oaks on shallow-soiled, droughty sites. The loss of overstory oaks results in reductions in the stand's acorn production potential and promotes the release of shade tolerant advance reproduction.*

To counter the succession of oak forests toward shade tolerant species and to create conditions favorable to oak regeneration, shelterwood harvesting has been recommended (Sander 1979, Hannah 1987). The advantages of shelterwood management of red oak derive from the presence of a significant overstory canopy. Initial cuts that remove a portion of the stand basal area can promote the growth of existing oak advance reproduction while providing sufficient shade to reduce the growth of its competitors.

The manipulation of overstory and understory vegetation under a shelterwood prescription also aids in the establishment of new reproduction. However, shelterwood systems that involve overstory harvests alone have not been consistently successful in regenerating oak forests (Sander and Clark 1971, McGee 1975, Rudolph and Lemmien 1976, Loftis 1983, Martin and Hix 1988). Regeneration to oak under a shelterwood system has succeeded only when adequate oak reproduction is present and when competition from other understory vegetation is controlled or minimal (Johnson and Jacobs 1981, Wolf 1988, Johnson et al. 1989, Wydeven 1989, Loftis 1990b, Crow 1992).

The purpose of this report is to review the scientific literature on red oak biology and silviculture as it pertains to the use of shelterwood systems in oak regeneration and management. Sections 3.0 through 5.0 synthesize a large body of literature on the ecology, physiology and reproductive biology of red oak. The importance of seedling ecophysiology in shelterwood management of red oak is illustrated with preliminary results from a field experiment being conducted near Foymount, Ontario. Section 6.0 provides operational recommendations and guidelines for shelterwood management of red oak in Ontario based upon the best information currently available.

2.0 Ecophysiology, succession and silviculture

Through natural selection, vascular plant species have evolved physiological traits and life history characteristics that are adaptive to general combinations of habitat disturbance and environmental stress. "Disturbance" refers to events at various spatial scales that limit plant biomass accumulation through its partial or total destruction. Disturbance can initiate succession and includes various agents: fire, wind, flooding, soil erosion, death of older individuals, herbivores, insects, diseases, human activity, etc. "Stress" is defined here as suboptimal environmental conditions that reduce physiological activity and growth of plants. Under severe stress, irreversible injury and mortality can occur.

Stresses or resource limitations on a site may be biotic or abiotic in origin. Biotic stress agents include insects, pathogens, herbivorous wildlife, plant competition and human activity. Abiotic stress refers to conditions of the physical microenvironment (e.g., high temperature) unfavorable to physiological processes. The relative intensity and duration of abiotic stress are influenced by the climate, topography, geology and soil properties of a given habitat. The vegetation and the disturbance regime of the habitat can modify the intensity, duration and effects of these stresses, particularly at the microenvironmental scale.

Three primary ecological strategies by which higher plant species can be generally classified have been proposed (Grime 1977). A matrix that combines the 2 extremes (high and low) of stress and disturbance intensity can be used to identify 4 general habitat types and which of Grime's 3 evolutionary ecological strategies is associated with dominance in each habitat type (Table 1).

Table 1. *Ecological strategies of vascular plants growing in habitats of different stress and disturbance intensity (Grime 1977).*

Stress level	Disturbance intensity	
	Low	High
Low	Competitive strategy	Ruderal strategy
High	Stress tolerant strategy	No viable strategy

A combination of high stress and high disturbance intensity is too extreme to support an abundance of higher plant life and no viable ecological strategy exists. A combination of low stress and low disturbance favors plant species with the "competitive" strategy, whereas high stress, low disturbance habitats favor a "stress tolerant" strategy. A "ruderal" strategy describes species that are best suited to aggressive occupation of habitats characterized by low levels of stress and high frequency of disturbance. Several general characteristics of plants in each category are listed in Table 2.

Tree species that have developed a competitive strategy are early successional, shade intolerant species that are adapted to dominate on open, more productive sites. These species exhibit rapid early growth rates after disturbance, an adaptation for the capture of large amounts of above- and belowground resources from newly available growing space. Competitive species also have a well developed capacity to modify morphology and physiology in response to transient changes in resource availability (i.e., phenotypic plasticity). This is adaptive to early successional habitats characterized by greater variability in environmental factors such as light, temperature, humidity and wind (Bazzaz 1979). For example, when shaded, these species invest a larger percentage of their total carbohydrate in production of tall shoots that support large leaf areas above the understory canopy. This increases the amount of shoot biomass actively involved in light harvesting and photosynthesis. These species are quite demanding in terms of site requirements and exhibit a proportionally large decrease in growth rate when exposed to stress.

The stress tolerant strategy characterizes many mid- to late-successional species of intermediate to high shade

Table 2. *Some general characteristics of plant species in relation to their ecological strategy (Grime 1977).*

Ecological strategy		
Competitive	**Stress tolerant**	**Ruderal**
• maximum rate of resource capture	• ability to store and conserve resources	• aggressive colonizer after disturbance
• rapid growth rate	• slow growth rate	• rapid growth rate
• high phenotypic plasticity	• low phenotypic plasticity	• short life cycle
• stress intolerant	• evergreen leaf habit	• seed remains viable in soil seed bank for long periods
	• stress tolerant	• large proportion of annual production invested in seeds

Table 3. Ecophysiological and reproductive characteristics of forest tree species associated with red oak in Ontario[*].

Species	Shade tolerance	Early height growth	Site needs	Years between good seed crops	Vegetative reproduction[a]	Delayed germination
Red oak	Medium	Medium	Medium	3-5	High	None
Sugar maple	High	Low-Medium	High	3-7	Medium - small stumps	None
Red maple	Medium	Medium	Low	1	High	2 years
Striped maple	High	Medium	Medium	------	Medium	2 years[b]
American beech	High	Low	Medium	2-5	Low - stumps Medium - root suckers	2 years[b]
Yellow birch	Medium	Medium	Medium-High	1-3	Low	2 years[b]
White birch	Low	High	Medium	2-4	Medium - small stumps	2 years[b]
Aspen	Low	High	Low	4-5	High - root suckers	2 years[b]
Black cherry	Low	High	Medium-High	3-4	High	3-5 years
Pin cherry	Low	High	Low	------	Medium	>30 years
Basswood	Medium-High	Medium-High	High	1-2	High	3-5 years
White ash	Medium	Medium	High	2-5	Medium-High	2 years[c]
Jack pine	Low	Medium	Low-Medium	3-4	None	None[d]
Red pine	Low	Low-Medium	Low-Medium	3-7	None	None
White pine	Medium	Medium	Low-Medium	3-5	None	None
Eastern hemlock	High	Low	Medium	2-4	None	None

[*]/ A dashed line is used where no information is available.

[a]/ Sprouting from stumps, seedling root collars and root suckers are reported separately where necessary.

[b]/ Very low percent delayed (2nd year) germination has been reported. Seed bank is not a significant regeneration strategy.

[c]/ Delayed germination may be as great as 75%.

[d]/ Seed may remain viable in serotinous cones for 5-10 years.

tolerance. These species have an inherently slow early height growth rate and an exceptional ability to store and conserve resources. The presence of a forest canopy in mid- to late-successional habitats creates an understory with comparatively little fluctuation in environmental conditions. As a consequence, stress tolerant species exhibit relatively low phenotypic flexibility. Instead, they are adapted for survival in the forest understory, and rapid height growth following the formation of canopy gaps. The length of time a species can survive in the understory depends on its shade tolerance. Very shade tolerant species (e.g., sugar maple) can survive longer in the understory than mid-tolerant species (e.g., red oak). Physiological adaptations to certain stresses are often interrelated such that drought tolerant species also possess the capacity to withstand low soil fertility, resist low temperature injury, etc.

Species of the ruderal strategy are typically herbaceous annuals or short-lived perennials, but perennials are much more important in forest ecosystems. These species are adapted for aggressive invasion of productive, disturbed sites. Although relatively short-lived, these species are capable of rapid biomass production and precocious development of large amounts of mature seed that remain viable in the soil for long periods. For example, seeds of the raspberries (*Rubus* spp.) remain dormant in the seed bank in excess of 50 to 100 years until a disturbance creates a suitable environment for germination and survival. Colonization after disturbance by other ruderal species, such as bracken fern (*Pteridium aquilinum* L.) depend more on vegetative reproduction by a large, well established network of underground rhizomes.

The silvical characteristics of red oak and its common associates in Ontario are presented in Table 3. Species are described with respect to their tolerance of resource limitations and their reproductive characteristics. It is difficult to group these species by a single ecological strategy. In nature, plant species may possess features of more than one ecological strategy but one usually predominates. Pin cherry (*Prunus pensylvanica* L.) is best described by the competitive strategy, but delayed seed germination is a trait consistent with the ruderal strategy.

Succession may be viewed as a gradient in time, characterized by the continuous colonization and mortality of species populations (Pickett 1976, Bazzaz 1979). Succession is initiated by disturbance, followed by an establishment phase that depends strongly on site conditions, initial species composition and the ecological strategy of the early colonists. Thereafter, temporal changes in species composition and community structure during succession are the result of disturbance regime, stress tolerance adaptations, reproductive characteristics, competition and changes in habitat microenvironment.

The physiological and life history characteristics (i.e., ecological strategy) of plant species are of central importance to forest succession. Temporal changes in the physical (e.g., light quantity, soil moisture, etc.) and biotic environment (e.g., insect and wildlife populations involved in herbivory, pollination, seed dispersal, etc.) of the developing forest stand lead to the mortality and decreased abundance of species poorly adapted to the current environment. Generally speaking, species of the ruderal and competitive strategy are slowly replaced over time by species of the stress tolerant strategy.

Ecologically-based forest management practices can be developed through the integration of the regeneration ecology and physiology of target and noncrop species with operational objectives. The shelterwood system is well suited to management of red oak and other midtolerant forest tree species. The creation of canopy gaps by partial cutting coupled with site preparation and tending treatments can be used to emulate the natural disturbance regime, improve acorn production and create a favorable microenvironment for the establishment and growth of red oak seedlings. The amount of basal area removed in initial and subsequent harvests and the site preparation applied can be tailored to the species composition and site productivity of the stand being treated. In this manner, regeneration of red oak can be favored over that of the competition. It is our hope that the discussion of red oak ecophysiology (sections 3.0 and 4.0), regeneration ecology (section 5.0) and their relationship with shelterwood management (section 6.0) assists researchers and field foresters in the further use and development of biologically sound silvicultural prescriptions for the regeneration of red oak.

3.0 Growth characteristics

3.1 Shoot growth

The inherent shoot development pattern of a tree species can be broadly classified as fixed or free growth (Kramer and Kozlowski 1979). The first spring shoot growth flush of trees in both general categories evolves from leaf and stem units contained in overwintered buds that formed during the previous growing season. Tree species with a fixed shoot growth habit (e.g., white pine, sugar maple) produce only a single shoot flush in the spring. Some species with the fixed growth habit, such as red oak, exhibit recurrent or episodic flushes of shoot growth. In these species, the terminal bud formed after spring flushing of the preformed bud will also elongate if exposed to optimal growth conditions (Reich et al. 1980, Dickson et al. 1990). Species with a free growth habit (e.g., poplar and birch) exhibit an initial spring growth flush of the preformed bud followed by formation of additional stem and leaves from primordia that are initiated during the year of elongation.

The periodicity of bud break and leaf emergence is under both environmental and genetic control. In the spring, the cumulative thermal sum (e.g., degree-hours, degree-days) to which buds are exposed largely controls the timing of leaf emergence in temperate deciduous forest species. Seasonal timing of bud break may also vary with the microenvironment in which the buds were formed. Red oak seedlings grown under the shade of an overstory canopy exhibit earlier spring shoot flushing than seedlings growing on exposed clearcut sites (McGee 1975).

Earlier bud break may allow understory seedlings to take advantage of the brief period of high light availability before the overstory leafs out. However, these seedlings may be predisposed to spring frost damage where harvesting has removed the protective overstory. Winter logging that removes a significant amount of the overstory cover may increase the risk of frost damage to previously shaded oak advance reproduction in the first growing season after harvest (McGee 1975).

The spring growth flush of red oak consists of elongation of the new shoot, emergence and expansion of leaves, and formation of the terminal bud. This is followed by a period of little shoot activity, the "lag" phase. The beginning of this lag phase coincides with the preferential allocation of photosynthate to the root system and enhanced root growth activity. This developmental sequence has important implications for planted oak in artificial regeneration efforts (section 5.2).

Additional episodic shoot flushes, separated by periods of relatively high root growth, occur in red oak under favorable environmental conditions. These alternating periods of relatively high root and shoot activity are accompanied by a large percentage (>90%) of current photosynthate being transported to the roots and shoots, respectively (Hanson et al. 1986, Dickson et al. 1990). Multiple flushes commonly occur in red oak seedlings grown under optimal conditions in greenhouses and nurseries (Phares 1971, Farmer 1975). Recurrent shoot flushing is less common in nature and occurs more frequently in sprouts that arise from cut stems of advance reproduction or overstory trees than in uncut seedlings, saplings or mature trees (Reich et al. 1980, Dickson et al. 1990, Crow 1992).

3.2 Root growth

Red oak in particular, and oaks in general, are characterized by well developed, deeply penetrating taproot systems. The taproot of red oak seedlings may attain a depth of 45 cm in the first year, with 18 cm formed before the appearance of the first leaves (Holch 1931, Bourdeau 1954, Lyford 1980). Twelve to 18 first-order lateral roots per cm of taproot length can be produced by red oak seedlings in a single growing season (Lyford 1980). On deeper soils, the root systems of 1-year-old red oak seedlings may have taproots up to 1.8 m long, and a lateral root spread of 1 m (Holch 1931). Many of the original lateral roots die back by ages 3 to 5, with fewer, woodier lateral roots remaining to form the structural framework of the root system (Lyford 1980).

Young oak seedlings preferentially allocate a larger proportion of photosynthate to root growth than to stem and foliage growth (Dickson et al. 1990). Red oak seedlings exhibit a rather conservative shoot growth habit, with suboptimal environmental conditions also slowing shoot activity and shifting the allocation of current photosynthate to the roots. This carbohydrate both supports continued root growth and is stored in the taproot for future use in shoot growth.

The preferential maintenance of root growth over shoot growth is an important ecological adaptation that enables red oak to occupy drier, less productive habitats and to persist in high disturbance environments. The development of seedlings with a large, physiologically vigorous root system and high root-shoot ratio is also a key factor in the capacity of red oak to resprout following shoot dieback (section 5.1.6, Figure 4). This large, expansive root system provides carbohydrates, water and nutrients in amounts required to produce and support a new shoot capable of multiple growth flushes.

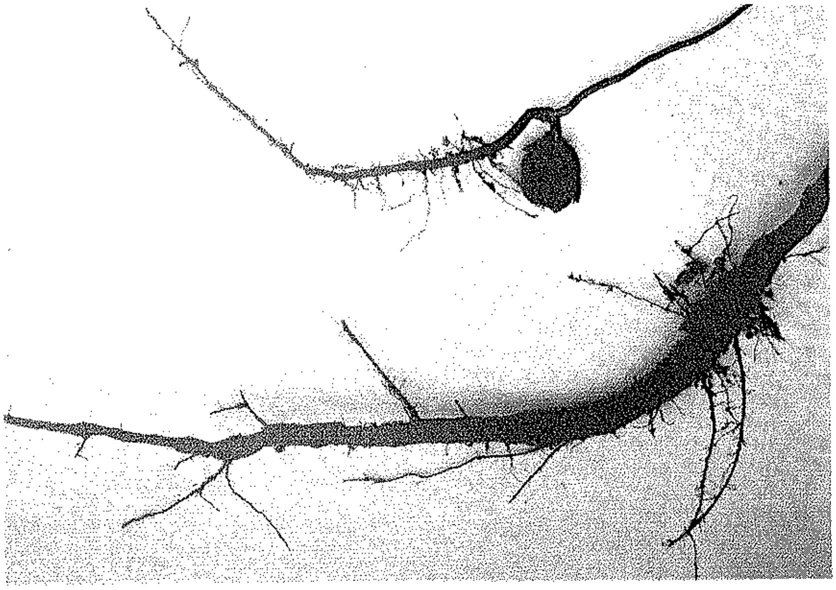

Figure 4. *Featured here are 2 root systems from natural red oak advance reproduction that developed in the understory of an uncut hardwood forest in Ontario. The 1-year-old root system (top) is compared to an 8-year-old root system on the bottom. Red oak preferentially stores carbohydrates in its roots. Over time, a large root system may develop that can support new shoot growth when the original shoot dies or is damaged.*

4.0 Environmental requirements and stress response

4.1 Light

Photosynthesis is the light energy-driven physiological process by which plants convert atmospheric CO_2 to carbohydrate. This depends on the gaseous diffusion of CO_2 through the stomata to internal leaf surfaces, and transport to sites of fixation in the chloroplast. Photosynthesis is limited by low intensities of photosynthetically active radiation (PAR), by stomatal closure and when chloroplast function is impaired by environmental stress. Net photosynthesis (P_n), or net carbon gain by plants, is equal to total photosynthetic CO_2 fixation minus respiration.

Red oak has an intermediate rate of P_n as compared with its common, co-occurring species (Walters et al. 1993, Ashton and Berlyn 1994). Red oak P_n is generally less than for herbaceous species and early successional, shade intolerant woody species, but greater than for more shade tolerant species (Loach 1970, Bazzaz 1979, Bazzaz and Carlson 1982).

Net photosynthesis increases linearly with PAR to a saturation point where it remains stable or increases slightly with further increases in light intensity (Figure 5). In the dark (PAR=0), P_n is negative in value and equal to the respiration rate. With increasing light intensity, the light compensation point is attained (PAR where P_n=0). As light intensity increases above the compensation point, the linear increase in P_n per unit PAR is indicative of quantum efficiency, i.e., the efficiency of light energy utilization in photosynthesis. Light saturation of P_n in red oak generally occurs at 20 to 40% of full sunlight (Teskey and Shrestha 1985, McGraw et al. 1990, Ashton and Berlyn 1994). Shade tolerant, later successional species typically have lower respiration rates, light compensation points, PAR at light saturation and maximum P_n, but higher quantum efficiency than more shade intolerant species (Bazzaz 1979).

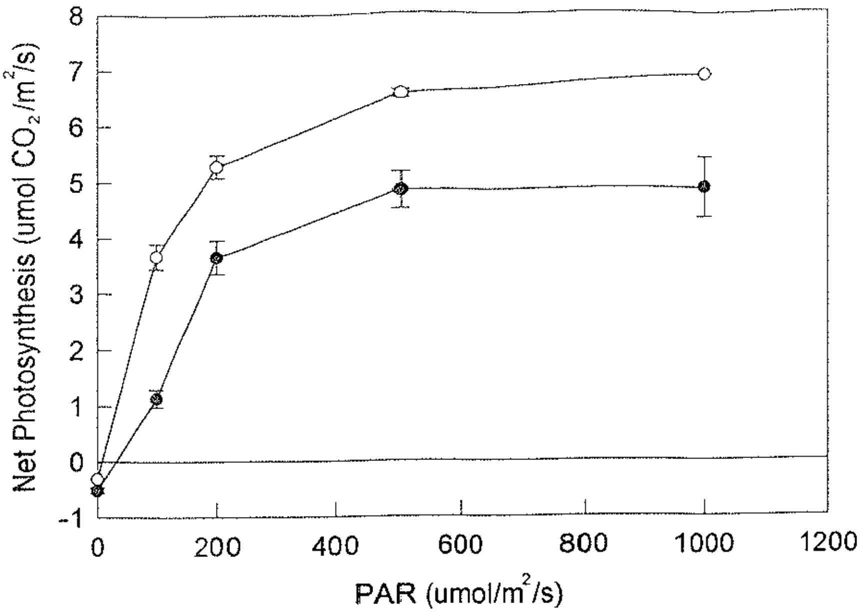

Figure 5. *The relationship between net photosynthesis and light intensity (expressed as PAR) for red oak seedlings grown under 65% (solid circles) and 5% (open circles) sunlight. Each point is the mean (± standard error) of 3 to 5 seedlings. Full sunlight is approximately 2,000 umol/ m^2 /s.*

The relationship between P_n and PAR differs slightly between red oak seedlings grown under high light and shaded conditions (Figure 5) (Loach 1967, McGraw et al. 1990). Adaptation to shade is associated with decreased respiration rates, a lower light compensation point, lower light saturation points and higher quantum efficiency (Figure 5). These photosynthetic adaptations allow shaded oak seedlings to operate more efficiently under low light. Higher light saturated P_n and more rapid stomatal and photosynthetic response to changes in PAR in shaded seedlings allows them to take advantage of brief, periodic sunflecks in the forest understory (Woods and Turner 1971, Bazzaz 1979).

Growth and survival of red oak in shaded microsites depends upon photosynthetic CO_2 fixation exceeding the respiratory requirements of seedlings. The average minimum light level required by red oak seedlings to produce enough carbohydrate to meet the energy needs of existing tissues (i.e., the light compensation point) is about 2 to 5% of full sunlight (Hanson et al. 1987). Smaller seedlings generally have lower respiratory maintenance demands and can survive longer under low light conditions than larger seedlings (Hanson et al. 1987). Although survival of red oak seedlings at this very low light level may be possible, sufficient carbohydrate to support the production of new tissue requires greater light availability. Gottschalk (1994) reported that positive shoot growth rates of red oak seedlings require light levels above 20% of full sunlight. Shelterwood cuts should increase understory light to at least this level to promote the growth of oak reproduction (Gottschalk 1994).

The regeneration of red oak depends more upon light availability than on any other environmental resource (Abrams 1992). Red oak is ranked as intermediate in shade tolerance and generally shows increased height and diameter growth at up to 50 to 70% of full sunlight (Musselman and Gatherum 1969, Phares 1971, Gottschalk 1994). Shade generally decreases the total plant and root biomass of red oak seedlings, but the root-shoot balance and other seedling morphological traits are relatively unresponsive to light availability (Kolb and Steiner 1990, Kolb et al. 1990, Latham 1992, Walters et al. 1993). The allocation of a large percentage of the total available carbon to roots (section 3.2) is apparently maintained even under shaded conditions where more intolerant species exhibit reduced root-shoot ratios and enhanced investment in the production of foliage.

Leaf anatomy and morphology of red oak seedlings are more responsive to light than is seedling morphology. Foliage that forms under full sunlight is thicker and heavier (grams dry weight per unit leaf area), develops more cells that are involved in photosynthesis, and has greater numbers of stomata per unit leaf area (Kolb et al. 1990, Latham 1992, Ashton and Berlyn 1994). Red oak seedlings growing under shaded conditions also exhibit a more horizontal leaf orientation that increases their ability to harvest light (McMillen and McClenden 1979).

The capacity of heavily shaded seedlings to respond to additional environmental stresses may be reduced because of their inherently low vigor. For example, shaded red oak seedlings are less able to recover from defoliation by herbivores (McGraw et al. 1990, Byington et al. 1994). Seedlings growing in the understory also have lower root energy reserves and, therefore, a reduced potential for sprouting following shoot dieback (Parker 1979).

4.2 Water

The uptake of CO_2 through stomatal pores required for photosynthesis coincides with the diffusion of water vapor from the wet internal leaf surfaces to the atmosphere. Plants are thus confronted with the dilemma of harvesting CO_2 for photosynthesis while minimizing water loss through transpiration. During the day, transpiration generally exceeds the rate at which soil moisture is absorbed by the roots. The diurnal lag in absorption behind transpiration results in a reduction in leaf water content. At night, stomatal closure decreases transpiration to a negligible rate, and continued root water uptake acts to rehydrate plant tissues. Under environmental conditions of low soil moisture and/or high atmospheric evaporative demand (section 4.4), injurious water deficits may develop and inhibit many physiological processes (Kramer and Boyer 1995).

The oaks as a group are quite tolerant of drought, primarily due to their large root systems, leaf morphological characteristics that reduce transpiration, and the ability to maintain gas exchange and P_n to comparatively low levels of leaf water status (Abrams 1990). The development of a strong taproot system in oaks provides them access to moisture from deep soil layers, which is less available to more shallow rooted species. Although red oak is one of the least drought tolerant of the upland oaks of eastern North America (Bourdeau 1954, Seidel 1972, Kleiner et al. 1992), it is more drought adapted than many co-occurring species such as the poplars, white birch, and sugar maple (Bahari et al. 1985, Martin et al. 1987).

Despite red oak's moderate drought tolerance, on comparatively dry sites or during seasonal periods of low soil moisture availability, rates of leaf gas exchange decline (Bahari et al. 1985), shoot and root growth of seedlings decrease (Larson 1980, Pallardy and Rhoads 1993), and the risk of mortality increases (Wright et al. 1989, Thompson and Schultz 1995).

Red oak seedlings also exhibit lower leaf area and new root production, delayed bud break, reduced shoot elongation and increased shoot dieback when exposed to water stress (Larson and Whitmore 1970, Larson 1980, Wright et al. 1989). Droughted red oak seedlings also produce stems with less xylem tissue and fewer and smaller vessels, the sole pathway for stem water movement in this species (Larson and Whitmore 1970, Shumway et al. 1993). The negative effects of drought are greater for recently transplanted stock than for established seedlings because of initially poor contact between the roots and the soil after transplanting.

Red oak has a ring-porous vascular anatomy and is quite susceptible to catastrophic dysfunction of its axial water transport system. Drought stress results in increased tension in the water in the xylem vessels that can cause these water columns to break and vessels to fill with air (Cochard and Tyree 1990). This "cavitation" (formation of embolisms in the xylem) results in a largely irreversible loss of stem water transport capacity. Vessels of larger diameter, characteristic of the earlywood of red oak and other ring-porous species, are generally more susceptible to cavitation than are the smaller diameter vessels of the latewood or of diffuse-porous species (e.g., sugar maple) and the tracheid-type vascular elements of conifers (Cochard and Tyree 1990, Sperry and Sullivan 1992). The hydraulic conductivity of current year's shoots of red oak seedlings may decrease by 20% in late summer due to drought-induced cavitation (Cochard and Tyree 1990).

Hard frosts in the fall cause additional cavitations when dissolved air in the xylem sap is forced out of solution during freezing of the water. This second source of cavitation further reduces hydraulic conductivity to 5 to 35% of the initial value (Cochard and Tyree 1990). By the end of a growing season, most of the water transport potential in oak stems may be lost. As a consequence, cambial activity must resume in the spring before leaf emergence to produce a new growth ring that re-establishes a water pathway between the roots and the new shoots.

The presence of an overstory canopy can influence soil moisture availability, and the rate of water stress development and its effect on the physiological processes of oak regeneration (section 4.7). Soil moisture content is generally higher after partial or complete overstory removal due to reduction in both rainfall interception by the canopy and total stand transpiration (Crunkilton et al. 1992, Breda et al. 1995). More open conditions, however, result in greater atmospheric evaporative demand and transpiration. Seedlings in the forest understory are exposed to a more humid environment that reduces transpiration, but water deficits may develop due to intense root competition for soil moisture.

Both beneficial and negative effects of forest overstories on oak seedling water relations have been reported. For example, low P_n of underplanted red oak seedlings in the shaded understory of a shelterwood reduced the supply of carbohydrate needed to support new root growth (Crunkilton et al. 1992). As soil moisture became limiting in the drier summer months, these seedlings lacked the root system needed to avoid injurious leaf water deficits. These underplanted seedlings also exhibited greater seasonal water deficits than those planted in a clearcut. Conversely, red oak seedlings underplanted in a shelterwood had a lower incidence of drought-induced leaf abscission than seedlings in a clearcut due to the moderating effect of the overstory on seedling water use (Linit et al. 1986). Underplanted seedlings in uncut or shelterwood stands may also exhibit the adverse physiological effects of transplant shock for a much shorter time than those planted in clearcuts (Johnson 1994b; Parker and Dey, unpubl.). This is likely due to reduced transpiration inshaded, more humid understory locations (section 4.7).

4.3 Nutrients

Red oak exhibits its best growth on deep, well-drained, loamy to silty, clay loam soils with a thick A horizon (Sander 1990). Although the growth potential of red oak improves on more productive sites with high soil fertility, the species has relatively moderate nutrient requirements. Height growth rates and the leaf area of red oak seedlings increase with high soil fertility but biomass production increases to a much lesser degree than for early successional species of the competitive strategy (Kolb et al. 1990, Truax et al. 1994). However, on less productive sites, conservative growth rates of red oak decrease much less than for pioneer species due to the stress tolerant ecological strategy of oak. Seedling morphology is relatively unresponsive to soil nutrient availability, although higher root-shoot ratios associated with reduced shoot biomass sometimes occur with low soil fertility (Kolb et al. 1990, McGraw et al. 1990, Latham 1992).

4.4 Temperature

Plant physiological processes have temperature optimums as well as a range within which normal functioning occurs. Significant deviation from optimum air (T_a) and soil (T_s) temperatures reduces the rate of these processes. For example, the maximum P_n of red oak was found to occur near 26 °C and declined at leaf temperatures above and below this value (Chabot and Lewis 1976, Hinckley et al. 1978). Bud break, shoot elongation and root growth are delayed by lower-than-normal spring temperatures, and suboptimal T_a and T_s reduce seedling growth (Larson 1970, Farmer 1975). Soil temperatures below 13 °C decreased the number of new roots produced and the rate of shoot elongation in 1+0 red oak seedlings (Larson 1970). Low T_s also negatively affects seedling water relations by reducing root hydraulic conductivity and water uptake.

Air and soil temperatures, and their diurnal variation in the understory, are reduced by the presence of forest canopies as compared with more exposed sites (section 4.7). Because of the moderating influence of forest canopies on understory temperature, the use of shelterwood systems for management of red oak may provide an additional advantage to this species by reducing the occurrence of radiational frost and injuries related to low temperature in the late spring (Zasada, unpubl.). This may be particularly important in Ontario, as the frost tolerance of red oak roots and shoots is lower than that of several associated species (Calme et al. 1994, 1995; Zasada, unpubl.).

Air temperature has a significant influence on seedling water relations through its effect on humidity. The saturated water vapor pressure (e_s) of the air increases exponentially with T_a. As a result, the vapor pressure deficit (VPD) of the air, the difference between e_s and the ambient atmospheric vapor pressure (e_a), also generally increases with T_a. Vapor pressure deficit is a useful expression of the evaporative demand of the atmosphere. The transpiration rate of plants increases with VPD, and indirectly with increased T_a. As forest canopies moderate T_a, they create a more humid (lower VPD) microenvironment. Consequently, the transpiration rate is typically lower, and midday leaf water status higher, for understory seedlings (section 4.7).

4.5 Herbivory

Insect defoliation represents a selective stress imposed on red oak reproduction (Figure 6). Many insect species prey on the foliage of oak seedlings (Linit et al. 1986, Galford et al. 1988). The source and severity of predation depend upon the insect community present, the total insect population of a microhabitat and the cyclical nature of some insect populations.

Reductions in leaf area through defoliation will decrease the growth of red oak seedlings through reduced photosynthetic capacity, and changes in biomass allocation patterns and the root-shoot balance (Wright et al. 1989, McGraw et al. 1990, Byington et al. 1994). Plants that sustain high levels of defoliation have a reduced chance of survival (Wright et al. 1989). Mortality may result, in part, from reductions in seedling leaf area below some threshold value needed to maintain a positive carbon balance (i.e., photosynthesis > respiration).

The susceptibility of red oak seedlings to insect predation may vary with the local environment and between local oak populations. Red oak seedlings underplanted in stands thinned to 50 to 60% stocking experienced less insect defoliation than those planted in a clearcut (Linit et al. 1986). However, higher levels of defoliation-induced mortality in shaded seedlings have also been reported (McGraw et al. 1990, Byington et al. 1994). Seedlings of mother trees from more mesic, north-facing slopes have exhibited less foliar damage by insects than those from adjacent subpopulations, which suggests local genetic adaptation to herbivory in red oak (Sork et al. 1993b).

Insect defoliation of red oak seedlings results in the production of chemical compounds and structural features that reduce the digestibility of the leaves (Hunter and Schultz 1995). This herbivore defense mechanism is initiated by

Figure 6. *A variety of insects feed on the foliage of red oak. This stress causes reductions in growth and survival.*

defoliation-induced alteration in the carbon-nutrient balance of plants. Fertilization of red oak seedlings prevented the biosynthesis of defense compounds and resulted in greater damage by several insect species (Hunter and Schultz 1995). Therefore, red oak nursery stock with comparatively elevated nutritional status may sustain greater defoliation during the first year of outplanting than naturally regenerated seedlings (Parker and Dey, pers. observ.). Low seedling moisture status can also result in comparatively greater insect defoliation, perhaps due to a drought-induced reduction in the capacity to synthesize defensive compounds (Stowe et al. 1994).

Browsing by mammalian herbivores, such as the white-tailed deer (*Odocoileus virginianus* Zimmermann), can be a serious impediment to the establishment of red oak (Marquis et al. 1976, Inouye et al. 1994, Gordon et al. 1995). Mortality from browsing is greater in smaller seedlings, which may be related to the larger proportional reduction in total shoot biomass per unit tissue consumed in smaller plants (Inouye et al. 1994). Although red oak can resprout from dormant buds near the root collar after shoot predation, the sprouting potential depends upon the existence of sufficient root carbohydrate reserves to produce these new shoots (section 5.1.6). Defoliation has been reported to decrease root starch and sugar contents and therefore repeated browsing may reduce sprouting capacity over time (Parker 1979). These effects would be particularly harmful to shaded seedlings with lower carbohydrate reserves. The loss of shoot tips and terminal buds through browsing also results in growth reductions and imbalances due to altered hormonal relations between roots and shoots (Larson 1975, Byington et al. 1994).

4.6 Competition

Controlled environment and greenhouse studies provide useful, detailed information on plant responses to variations in single resources. However, growth, survival and species abundance in the field are governed by the availability of multiple resources and by a species' capacity to harvest these resources in a competitive environment. Competition, both within and between species, is therefore an important source of environmental stress that arises from the demands of neighboring vegetation for a shared, limited resource base.

Early in this century, a great deal of scientific investigation was directed towards identifying the environmental factors that limit growth in the forest understory. During this time, the importance of root competition for below-ground resources between seedlings and overstory and understory vegetation was recognized (Craib 1929, Korstian and Coile 1938). Seedling growth of some tree species in the forest understory was found to be limited more by root competition for water and nutrients than by low light levels (Shirley 1945).

The relative effects of competition for light and soil resources on seedling performance is habitat dependent. On more fertile, productive sites, shading and above-ground competition for light is more limiting to growth than root competition (Putz and Canham 1992, Wilson 1993, Wilson and Shure 1993, Gerry and Wilson 1995). On higher quality, more open sites, competitive species that exhibit rapid shoot growth and leaf area development are better adapted and overtop inherently slower growing stress tolerant species such as red oak (Hannah 1987). On these sites, competition from shade intolerant, pioneer species can severely inhibit the performance of red oak and other stress tolerant species (Figure 7) (Scholz and DeVriend 1957, Adams and Anderson 1980, Heiligmann et al. 1985).

On relatively poor sites, which are low in nutrients and soil moisture, root competition among neighbors is more growth limiting. These sites generally support less total plant biomass and leaf area, such that understory light levels are higher (Grime 1977). Therefore, seedlings with a large root system that is in balance with the shoot, and that have the capacity for conservation and storage of soil resources are better adapted to poor sites than are seedlings with large, vigorous shoots that are out of balance with their root systems (Gerry and Wilson 1995). The stress tolerant strategy of red oak is better suited to sites with lower productivity. In the absence of disturbance, larger amounts of taller red oak reproduction are typically found on drier, infertile sites with a south-facing aspect (Trimble 1973, Kays et al. 1985, Myers and Buchanan 1988, Dawson et al. 1990, Ward 1992).

Figure 7. *Pin cherry colonizes many hardwood sites in Ontario following major disturbances. It is characteristic of species that use the competitive ecological strategy. Pin cherry has rapid early height growth and quickly suppresses stress tolerant species such as red oak following major disturbances.*

The abundance of red oak advance reproduction is less related to seed production, dispersal and germination than to environmental effects on the growth and development of seedlings in the understory (Tryon and Carvell 1958, Pubanz and Lorimer 1992). Vegetation may facilitate germination and establishment by sheltering seedbeds and dampening extremes in microsite environment (Wood 1938). However, under conditions of severe competition and very low light levels, establishment and growth of oak reproduction are both reduced (Crow 1992, Pubanz and Lorimer 1992). As a result, red oak seedlings growing beneath well developed canopies are generally too small and too few in number to dominate the site following overstory removal (Figure 8). Although shading of regeneration is commonly viewed as the most important factor limiting red oak reproduction, the effects of root competition with overstory and understory vegetation have not been adequately examined (Kolb et al. 1989, Kolb and Steiner 1990).

Many field trials have been conducted to determine the relative influence of overstory and understory vegetation on the growth of red oak reproduction. Overstory thinning treatments that increased light levels to ≥35%, applied singly or in combination with understory

Figure 8. *Red oak advance reproduction in undisturbed, mature hardwood stands is usually small, often less than 15 cm tall.*

removal, have generally resulted in improved survival and growth of both naturally regenerated and planted seedlings (Beck 1970, Johnson 1984, Pubanz and Lorimer 1992). Greater light availability was also associated with larger seedlings, greater leaf areas and higher frequencies of multiple flushes (Crow 1992). In untreated stands, higher mortality, reduced height growth and increased incidence of shoot dieback were observed. Reduced height growth in heavily shaded understories may be the result of a larger investment of carbohydrate into roots than into shoots (Johnson 1984).

Understory competition is particularly harmful to oak reproduction on better sites (Hannah 1987, Pubanz and Lorimer 1992, Lorimer et al. 1994) or when it is dominated by intolerant species (Beck 1970). The removal of taller understory vegetation (>1.5 m tall) from mature oak stands was reported to improve the 5-year survival and growth of underplanted oak seedlings (Lorimer et al. 1994). The effects of these treatments were generally greater on a relatively productive mesic site where understory competition was more intense compared to a less productive drier site (Lorimer et al. 1994). Readers are referred to section 6.2 for a discussion of silvicultural options for controlling understory vegetation.

4.7 Ecophysiology and shelterwoods

The influence of shelterwood systems on the ecophysiology of oak regeneration is currently being examined near Foymount, Ontario. Bareroot (2+0) red oak seedlings were underplanted in a closed canopied, mature hardwood stand in the spring of 1994 and 3 cutting treatments were applied in the winter of 1994/95. Stands were left uncut or were thinned from below to 70 or 50% crown cover. The microenvironment and ecophysiological characteristics of planted red oak and small (i.e., 0.1 to 1.0 m tall) advance reproduction of red oak and sugar maple (the primary woody competitor) were measured during the 1995 growing season in stands of each cutting treatment.

Partial cutting treatments had a dramatic effect on the seedling microenvironment (Figure 9). Reducing crown cover to 70 or 50% increased light intensity, VPD (decreased humidity), T_a and T_s (at 5 cm). The range of diurnal variation of these environmental factors was also increased relative to the uncut stand (Figure 9).

Microenvironmental changes associated with stand cutting treatments had a significant effect on seedling gas exchange and water relations (Figure 10). Light intensity in the uncut stands at the time of physiological measurements (July 19, 1995) was very low and averaged 20 umol/m^2/s (ca 1% of full sunlight) (Table 4). Under this heavily shaded condition, P_n was reduced to about 18 and 25% of the maximum P_n for red oak and sugar maple, respectively (Figure 10a). Light intensities in both partially cut stands were near or above the saturation point for P_n of red oak. As a result, P_n of red oak seedlings were about 4 times higher than in the uncut stand. Net photosynthesis of sugar maple also increased under the more open canopies, but P_n rates were significantly lower than for planted and natural red oak seedlings. Similar trends were exhibited for transpiration (Figure 10b), a result of the higher PAR, T_a and VPD in the thinned stands (Table 4, Figure 9). Increased atmospheric evaporative demand and higher seedling transpiration in the partially cut stands were associated with more negative (but not injurious) midday leaf water potential (i.e., lower leaf water status) (Figure 10c).

The results of this study illustrate the tremendous influence of the forest canopy on seedling P_n and water relations the first growing season after cutting. Stand manipulations to reduce percent crown cover will influence, at least initially, many other environmental factors of potential importance to oak regeneration. For example, greater T_a and T_s will increase the decomposition rate of organic matter and the amount of available nutrients. Canopy manipulation will also likely influence resident herbivore populations and the incidence of acorn predation and browsing damage.

5.0 Oak regeneration ecology

Regeneration of a desired species or species mixture to an acceptable stocking of well spaced trees following harvest is an important operational objective. Effective use of natural regeneration requires the presence of sexually mature trees capable of producing a large number of seeds. Seeds must reach receptive seedbeds located in microenvironments suitable for successful germination and seedling establishment. Thereafter, seedlings must have sufficient resources to grow competitively.

Shelterwood systems can facilitate the production of seed, create favorable environments for germination, and promote the development of advance reproduction of a size and density adequate to respond rapidly to a final overstory removal (section 5.1.3). Underplanting red oak in shelterwoods may be used to establish or supplement advance reproduction where it is insufficient in size and number (section 5.2).

5.1 Natural regeneration strategies

The natural regeneration strategy of a species depends upon its genetic potential for: (1) production and dispersal of large amounts of viable seed, (2) the

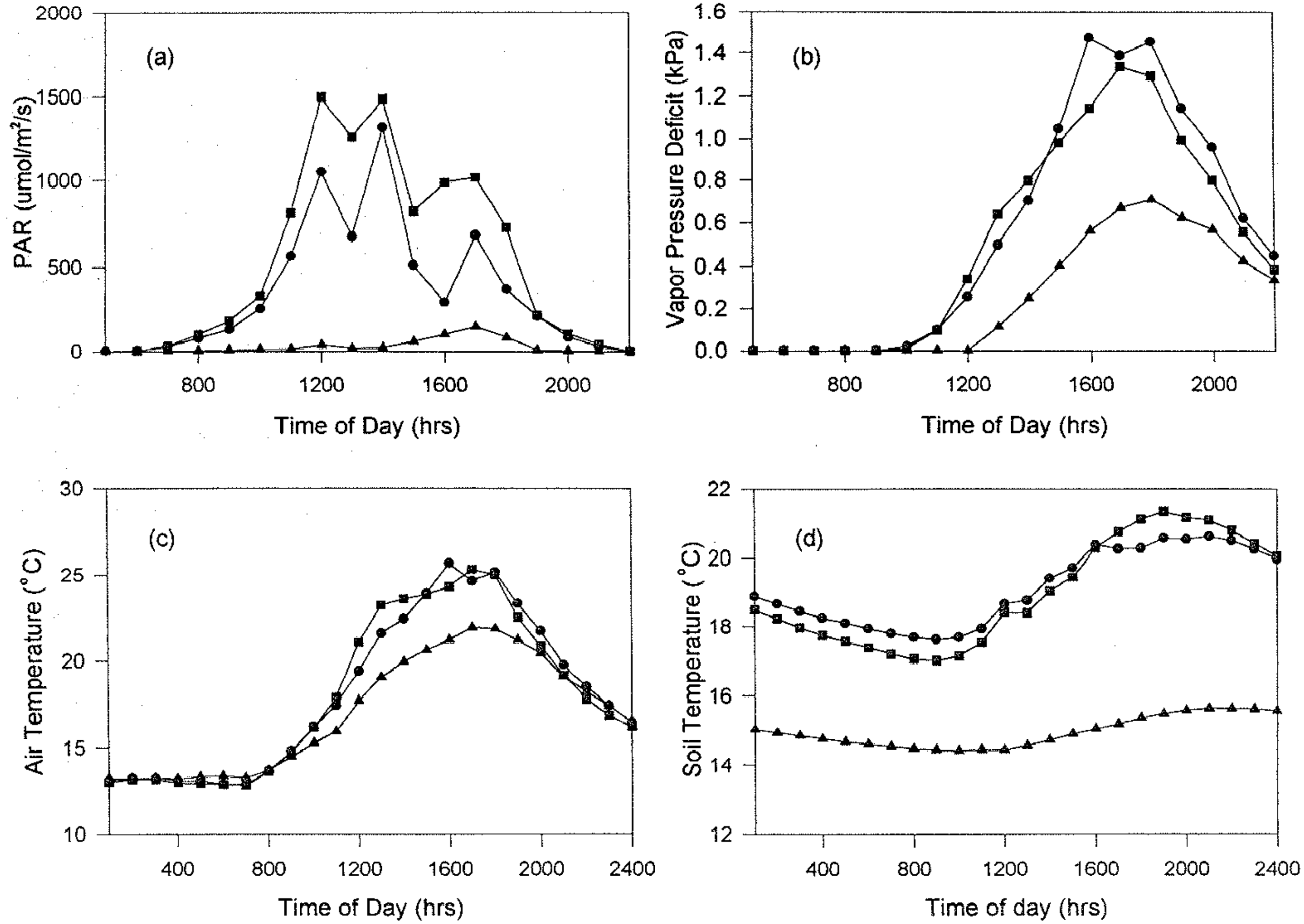

Figure 9. *Diurnal variation in hourly (a) photosynthetically active radiation (PAR), (b) atmospheric vapor pressure deficit, (c) air temperature and (d) soil temperature at a depth of 5 cm for the uncut (triangles), 70% (circles) and 50% (squares) canopy treatments near Foymount, Ontario. Data are presented for July 19, 1995.*

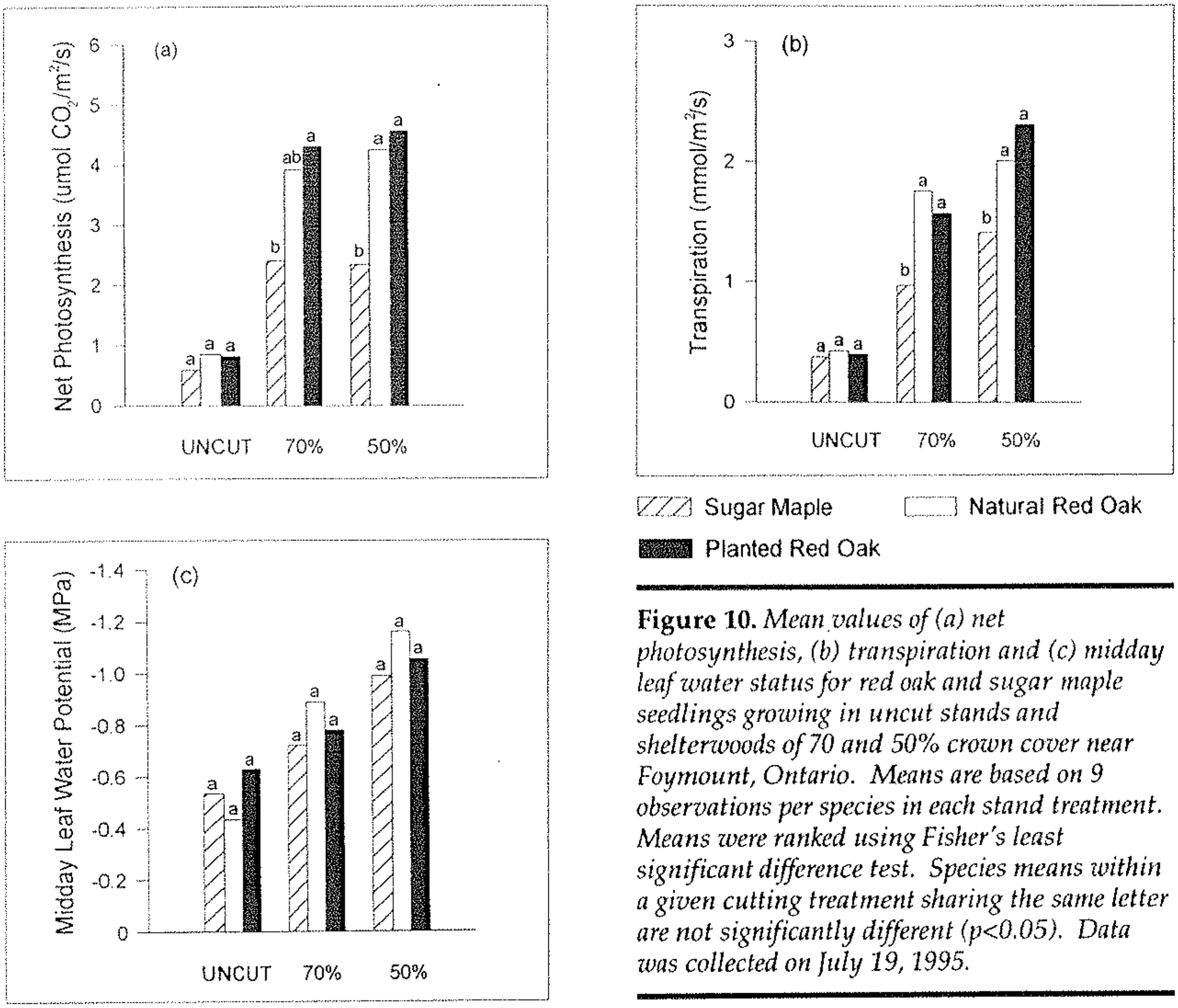

Figure 10. *Mean values of (a) net photosynthesis, (b) transpiration and (c) midday leaf water status for red oak and sugar maple seedlings growing in uncut stands and shelterwoods of 70 and 50% crown cover near Foymount, Ontario. Means are based on 9 observations per species in each stand treatment. Means were ranked using Fisher's least significant difference test. Species means within a given cutting treatment sharing the same letter are not significantly different ($p<0.05$). Data was collected on July 19, 1995.*

Table 4. *Average values of light intensity (PAR), air temperature (T_a) and atmospheric vapor pressure deficit (VPD) at the time of gas exchange measurements taken on July 19, 1995 in 3 cutting treatments near Foymount, Ontario.*

Crown Cover (%)	PAR (umol/m^2/s)	T_a (°C)	VPD (kPa)
uncut (100)	20.3(3.6)[1]	24.7(0.1)	1.31(0.46)
70	543.6(100.4)	29.4(0.3)	2.13(0.81)
50	977.9(128.9)	32.2(0.6)	2.67(1.61)

[1] / Each value is the mean and standard error (in parentheses) of 36 observations per cutting treatment.

retention of seed viability for many years in the soil seed bank, (3) growth and survival in the forest understory and rapid response to formation of canopy gaps (seedling bank) and (4) resprouting following the death of shoots or stems (bud bank). Tree species rely on one or more of these adaptations to colonize growing space created by disturbance.

The specific strategy possessed by a species shows a general relationship with successional status. Whitmore (1989) has proposed that forest tree species fall into 2 groups based upon their growth response following canopy gap formation. Small canopy gaps created by the death or removal of 1 to 3 members of the overstory favor the release of advance reproduction (seedling and bud bank) of more shade tolerant, mid- to late-successional species (Figure 11). These species grow slowly in the shaded understory but respond quickly in height growth and leaf area production to an improved light environment. Large gaps formed by the removal of many trees in the overstory, such as occurs after fire, logging (e.g., patch clearcuts) and massive insect outbreaks, are characterized by high light levels and, in some cases, thinner litter layers and increased mineral soil exposure. These large openings favor the invasion and establishment of shade intolerant, pioneer species with rapid growth rates (Figure 12). Colonization of these habitats occurs primarily through the production of large amounts of well-dispersed seed (e.g., white birch), exposure of the soil seed bank (e.g., *Prunus* spp.) and root suckering (e.g., *Populus* spp.).

5.1.1 Reproductive biology

Red oak is monoecious (male and female flowers occur on the same individual), and requires 2 growing seasons to complete the sexual reproduction cycle (Cecich 1994). Male and female floral structures develop between May and June from reproductive buds formed the previous growing season (Sork et al. 1993a). The male flowers originate from the axils of bud scales on the previous year's shoots. The female reproductive structures appear singly or in clusters in the leaf axils of current year's shoots. Pollination occurs from the spring to the early summer of the first year, but fertili-

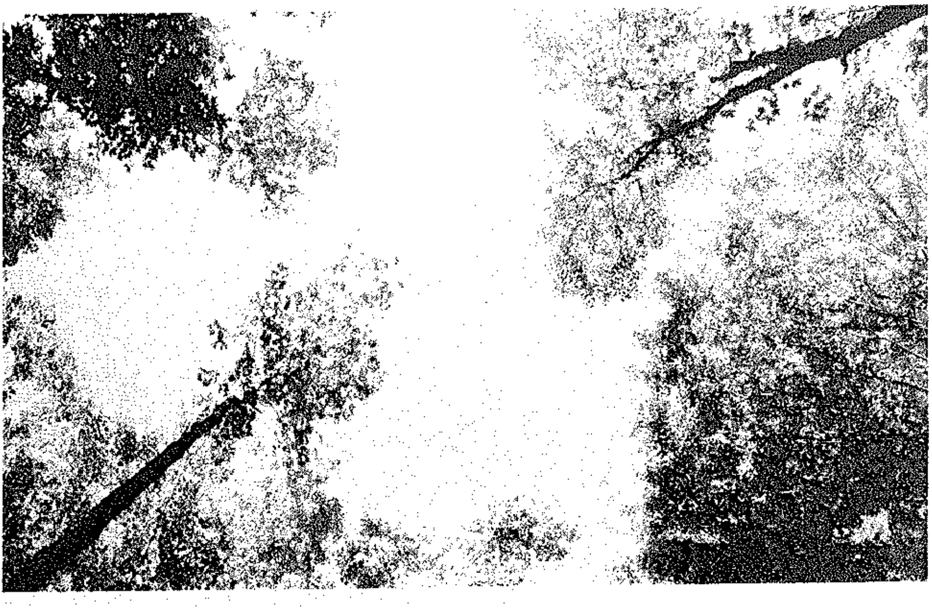

Figure 11. *Small canopy openings formed by the death or harvest of individual codominant or dominant trees create environmental conditions that favor the development of shade tolerant reproduction.*

Figure 12. *Clearcuts or large group selection openings promote the regeneration of shade intolerant pioneer species. Within 2 years after harvest,* Rubus *spp. dominated the reproduction in this Bracebridge stand.*

zation of the ovule, embryo development and the formation of fully mature acorns occurs the following growing season (Cecich 1994). Shedding of most of the mature acorns occurs from September to October, with poorly developed acorns abscising comparatively earlier (Downs and McQuilkin 1944).

Various environmental factors can affect the reproductive process within this 2-year period. Spring T_a is the climatic factor most strongly correlated with acorn yield, as cool temperatures may reduce the rate of emergence and development of the reproductive structures. Late spring frosts can also kill many flowers (Goodrum et al. 1971, Auchmoody et al. 1993, Sork et al. 1993a). Relative humidity can affect pollen release and dispersal. Relative humidities above 60% can inhibit splitting of the pollen sacs and the release of mature pollen, whereas comparatively low humidities can cause pollen sacs to dry, split and release pollen before it is mature (Cecich 1994). Wildlife may also destroy a substantial portion of the oak reproductive structures in certain years, because the floral structures provide a nutritious food source for many insects, birds and mammals (Hannah 1987, Cecich 1994). Generally, the number of acorns produced by a tree is related to the percentage of fertilized female flowers (and not the total number of flowers formed), and high early season damage and abscission of flowers are associated with small to moderate acorn crops (Sork et al. 1993a, Cecich 1994).

5.1.2 Acorn production

Red oak attains sexual maturity at age 25, but large acorn crops are generally not produced until age 50 (Sander 1990). As a group, the oaks produce very large seed crops on a cyclic basis. Red oak typically produces "bumper" crops of acorns on a 3- to 5-year cycle (Downs and McQuilkin 1944, Sork et al. 1993a). The annual variation in seed production is partially related to weather, but is primarily under genetic control.

Mast seeding (i.e., the cyclic production of large seed crops) is characteristic of species that provide an important food source for herbivores, and may represent an adaptation to this predation.

Overproduction of acorns exceeds the maximum potential consumption of seed by resident animal and insect herbivores (Downs and McQuilkin 1944, Sork et al. 1993a). These mast years ensure that some seed is available to germinate the following spring.

Acorn production can be quite variable among individual oak trees that occupy the same site. Some trees are inherently good acorn producers but others exhibit consistently poor acorn yields (Downs and McQuilkin 1944, Goodrum et al. 1971). Only a small percentage of the trees on a site may be good seed producers and these trees may yield bumper crops in different years. In the absence of a severe climatic event, total acorn crop failures within a given population are rare.

Although acorn crops have been characterized as "...sporadic, infrequent and unpredictable" (Auchmoody et al. 1993), good acorn production is associated with certain plant factors (Johnson 1994a). The maximum number of acorns per tree for red oak has been reported to increase with diameter up to 50 cm and decline thereafter (Figure 13) (Downs and McQuilkin 1944). Others have reported no strong relationship between acorn yield and stem diameter (Auchmoody et al. 1993, Sork et al. 1993a). Acorn production by red oak and other oaks is more closely correlated with crown size and, more specifically, with the amount of crown surface that receives full sunlight (Goodrum et al. 1971, Sork et al. 1993a, Johnson 1994a). Trees with near optimal diameter but with heavily shaded crowns exhibit comparatively lower acorn production (Goodrum et al. 1971, Johnson 1994a). Trees with exposed crowns may produce up to 5 times more acorns than those with shaded crowns (Johnson 1994a).

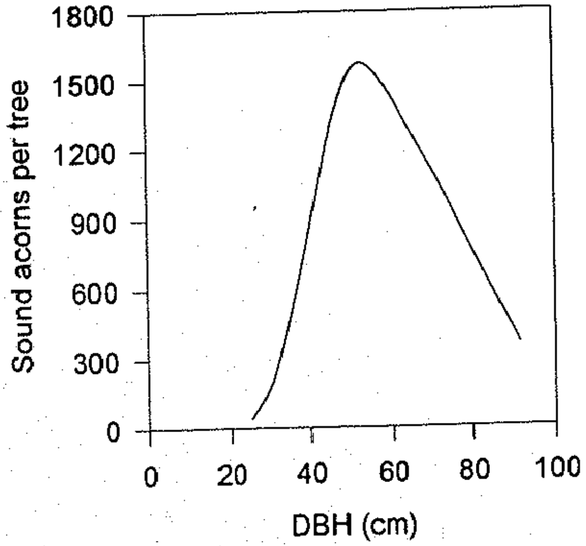

Figure 13. *Acorn production in red oak increases with tree diameter up to about 50 cm in dbh, beyond which it declines (adapted from Downs 1944).*

Partial cutting systems are particulary well suited to natural regeneration of red oak because of its relatively limited seed dispersal (section 5.1.4) and the moderating effect of an overstory canopy on the seedbed microenvironment. Johnson (1994a,b) has recommended that prescriptions to improve acorn production in shelterwood management should include: (1) identification of good seed producing trees before the first harvest, (2) retention of a good mixture of these trees after harvesting and (3) increased exposure of the crowns of these trees by thinning (Figure 14).

5.1.3 Acorn predation

Acorns are high in carbohydrates, fats and proteins and represent an excellent and important food source for wildlife (Korstian 1927, Goodrum et al. 1971,

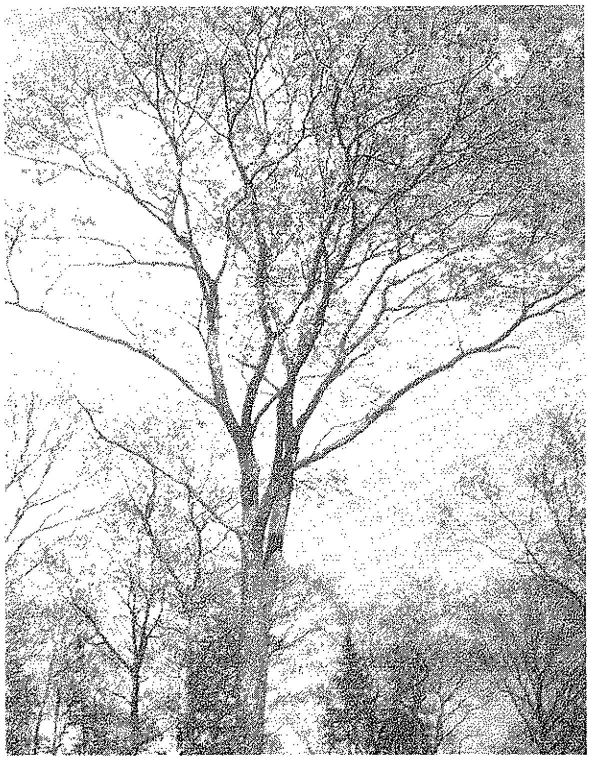

Figure 14. *Large-crowned red oaks that receive direct sunlight produce more acorns than oaks whose crowns are small or shaded. Dominant, full-crowned oaks should be retained after the initial shelterwood harvest. Identification of good seed producers before harvesting is recommended.*

Hannah 1987). Wildlife species that consume acorns include deer, squirrels, chipmunks, mice, ducks, turkey and jays (Hannah 1987). Small rodents are likely more responsible than large mammals for serious acorn losses, but this may not be true in areas with very large deer populations (Marquis et al. 1976, Gribko and Hix 1993, Auchmoody et al. 1994). In years of poor to moderate acorn crops, 90 to 100% of the available acorn supply may be consumed (Korstian 1927, Downs and McQuilkin 1944, Sork 1984, Johnson 1994b). In fact, habitats with poor oak reproduction were reported to have greater rates of acorn predation than sites with higher reproduction (Marquis et al. 1976).

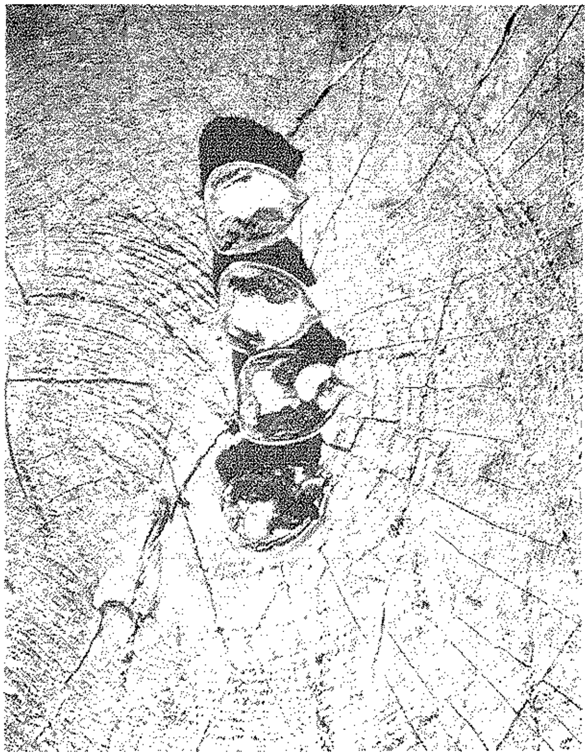

Figure 15. *Acorn insects damage a large proportion of the seed crop in most years. These red oak acorns have been severely damaged by larvae feeding on the cotyledon, radicle and plumule.*

Acorns and newly germinated seedlings also suffer heavy damage from a variety of insects (Figure 15). Insect damage is much greater in the litter layer, where most of these pests reside, than in acorns buried in the soil (Galford et al. 1991, Gribko 1995). Acorn weevils, moth larvae and gall-forming insects can destroy an entire acorn crop in poor seed years and a large percentage (20 to 50%) of the acorns in bumper crop years (Korstian 1927, Galford et al. 1988, Auchmoody et al. 1994). However, the results of a recent study by Steiner (1995) suggest that because of methods used in earlier experiments, acorn predation by insects may be much lower than previously reported.

Partial destruction of cotyledons by insect feeding may not significantly affect germination, but instead prevents normal seedling development and reduces seedling size and vigor (Korstian 1927, Gribko 1995). The condition of the cotyledons, however, is less important than damage to the radicle (root) and plumule (shoot), which nearly always results in mortality (Downs and McQuilkin 1944, Galford et al. 1991, Walters and Auchmoody 1993, Sonesson 1994).

Prescribed fire has been recommended as a means to remove the litter layer and thereby decrease rodent habitat, insect populations, and potential acorn predation (section 6.2.2) (Hannah 1987, Galford et al. 1988). Moderate to severe burns applied before acorn drop in the fall of good seed years may be particularly effective, as this is the peak period of acorn feeding by insects (Galford et al. 1988).

5.1.4 Acorn dispersal

Primary dispersal of acorns occurs by gravity and water (Korstian 1927). Because of their relatively large size, most acorns remain close to the parent trees, but some may be carried into microsite depressions by gravity and moving water. Although seed predation by some herbivores has a major negative impact on natural regeneration, others such as squirrels are important secondary seed dispersal vectors for oaks (Crow et al. 1994, Inouye et al. 1994). Wildlife species that store or "cache"acorns in the soil to provide a winter food source can improve the regeneration of oak by their "planting" of acorns. Burial of acorns in soil or beneath the litter layer protects seed from desiccation and further predation by other animals (Griffin 1971, Barnett 1977, Auchmoody et al. 1994). Jays may play a significant role in dispersal of smaller seeded oak species but the larger red oak acorns are generally avoided (Darley-Hill and Johnson 1981, Steiner 1995).

Oak seedling establishment from seed caching by wildlife likely results when herbivores die, forget the location of buried seed or when food demands are lower during mild winters. However, the impact of seed caching is likely significant only during mast years, when large amounts of seed are stored (Barnett 1977, Darley-Hill and Johnson 1981, Sonesson 1994).

5.1.5 Seedbed and germination requirements

The most important physical characteristics of the seedbed for germination of acorns and the establishment of seedlings are moisture, temperature, aeration and the mechanical strength of the soil (Korstian 1927). Exposure of acorns to the atmosphere during the winter and in the spring can reduce their moisture content and viability. Typically, acorns that are buried 3 to 5 cm in the soil and those in contact with mineral soil and beneath a layer of leaf litter show the best germination (Korstian 1927, Wood 1938, Sander 1979, Crow 1992). The presence of a layer of leaf litter, provided it is not thick enough (>5 cm) to damage emerging shoots, provides protection from desiccation and extreme fluctuations in T_a and T_s, and, as mentioned earlier, reduces predation by some animals (Korstian 1927, Wood 1938, Auchmoody et al. 1994). However, insect damage may be quite high in the litter layer (Galford et al. 1991). Soils below the litter layer may also be less compacted than exposed soil surfaces, allowing greater ease of root penetration (Korstian 1927).

Germination rate of acorns is best in soils that are neither too wet nor too dry, with T_a >10 °C at night and >18 °C during the day (Korstian 1927). Lower T_a delays germination. Higher T_a increases the germination rate but also increases the number of germinants that die due to desiccation (Korstian 1927).

Red oak acorns are quite large compared with the seeds of most co-occurring species in Ontario. The ecological advantage of big seeds derives from the beneficial effects of large energy reserves for germination and establishment. In shaded understory environments, developing seedlings of large-seeded species are less dependent on current photosynthate as an energy source for the production of new shoot and root tissues (Grime and Jeffrey 1965, Walters et al. 1993). The maximum height growth and survival of red oak grown under heavy shade was found to be greater than for other mid-tolerant tree species that have lower seed masses (Grime and Jeffrey 1965). Within each oak species, acorn mass varies and acorn size may be positively correlated with seedling shoot and root biomass. The silvicultural significance of the slight growth advantages provided by larger acorns, however, is questionable (Reich et al. 1980, Auchmoody et al. 1994).

5.1.6 Seedling and bud bank

The development of a large, healthy population of advance reproduction in the forest understory is a critical component of the natural regeneration strategy of red oak (section 6.3.1). Even-aged populations or "waves" of young red oak seedlings originate from bumper seed years. Because of the diminished role of fire in the forest, the slow early growth rate of red oak, and understory competition, some form of silvicultural intervention is necessary to cultivate this reproduction (section 6.2).

On more mesic sites, where competition is most intense, germination is greater than survival (Johnson 1994b). The presence of a forest canopy creates a microenvironment conducive to seed germination and seedling establishment, but the growth of this reproduction is inhibited by heavy shading (Figure 16). On these productive sites, low light availability typically results in mortality of the comparatively large cohort of young seedlings before the next bumper crop occurs. As a consequence, advance reproduction in mesic habitats derives from a single bumper crop.

Figure 16. *Heavy shading by the overstory and understory vegetation in undisturbed, mature hardwoods on fresh sites reduces light levels at the forest floor to less than 10% of full sunlight. The growth of red oak advance reproduction is inhibited by these low light conditions.*

Figure 17. *More light is available at the forest floor on drier sites because the overstory and understory vegetation layers are less dense and the stand's vertical structure is less complex than on fresh sites. Red oak advance reproduction have a greater likelihood of surviving and growing to larger sizes on these xeric sites than they do on fresh sites.*

On drier, less productive sites, microenvironmental conditions are less favorable for seed germination, but more light is available in the understory (Figure 17). As a result, fewer seedlings become established in these habitats, but the seedlings tend to persist in the understory for longer periods. Advance reproduction on these sites may represent several bumper crop years, as complete mortality of a given cohort is unlikely (Johnson 1994b).

Red oak seedlings that survive in the understory commonly experience recurrent shoot dieback and resprouting from buds near the root collar (Tworkoski et al. 1986). As a result, oak root systems gradually increase in size over time and are typically much older than the shoots they support (Liming and Johnston 1944, Merz and Boyce 1956). Oak reproduction from sprouts in Missouri had shoots 4- to 6-years-old and an average root system age of 24 years (Liming and Johnston 1944).

Adventitious buds located beneath the bark of oak stems remain dormant due to the inhibitory effects of auxins translocated downward from the terminal bud. Removal or death of the terminal bud releases dormant buds from apical dominance and stimulates the formation of new shoots. In seedlings that experience complete shoot kill due to environmental factors or fire, sprouts originate from buds near the root collar. Where partial shoot dieback or decapitation due to browsing by herbivores occurs, buds located at the highest position on the remaining living stem will sprout and become the new dominant leader. The shoot dieback and resprouting response of red oak also effectively reduces the probability of the development of advance reproduction with flat-topped crowns, which are associated with the lack of a dominant terminal shoot (Kelty 1988).

Sprouting from stumps of larger oak trees also occurs after stem removal during harvesting or when trees are damaged by wind or lightning (Figure 18). Stump sprouts are physiologically identical to seedling sprouts. Stump sprouts that originate from buds at or near the ground are more likely to survive and produce a straight, quality stem (Kelty 1988, Johnson 1994b). The likelihood of decay or breakage of these sprouts increases with increasing height above ground at which they originate.

Figure 18. *Stems of overstory red oak often produce stump sprouts after they have been cut in a harvest. The probability of producing sprouts and the subsequent growth of sprouts is related to the age and size of the parent tree (Table 5).*

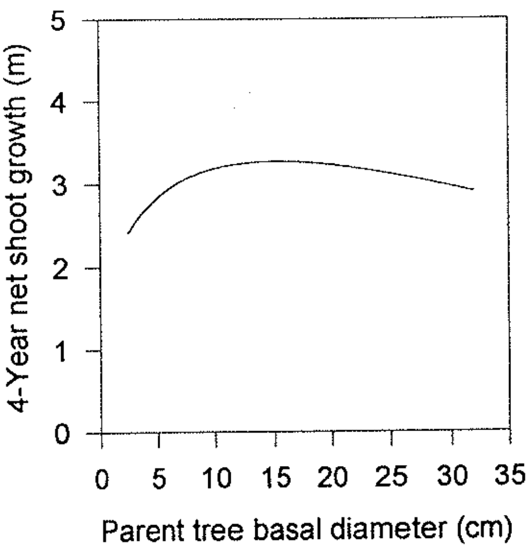

Figure 19. *Estimated net shoot growth of oak sprouts during the first 4 years after clearcutting in relation to the basal diameter of the parent tree (adapted from Johnson 1979).*

Stump sprouting frequency and growth increase with size of the parent tree up to a threshold, beyond which sprouting capacity declines (Figure 19) (Wendel 1975; Johnson 1977, 1979; Sander et al. 1984; Dey 1991). Sprouting potential and growth also decrease with increasing parent tree age (Table 5) (Johnson and Godman 1983, Stroempl 1983). Red oak is a prolific sprouter, especially in trees less than 60 years old. Oak larger than 50 cm in dbh sprout infrequently and oaks more than 80 years old have less than a 50% chance of producing a competitive sprout (Sander et al. 1984, Phillips and Shure 1990). Decreasing stump sprouting potential with increasing age and size may be due to the inability of dormant buds to penetrate the thicker bark of older trees.

The capacity for seedling and stump sprouting varies among species (Table 3) but also depends on a number of environmental and physiological factors (Solomon and Blum 1967, MacDonald and Powell 1985). The production of sprouts is governed primarily by the availability of the root carbohydrate reserves necessary to support the growth of these new shoots. Environmental factors that reduce photosynthesis and overall plant vigor may decrease the root energy reserves, and thereby the number and size of sprouts produced. Heavily shaded advance reproduction and large trees weakened by gypsy moth defoliation, oak decline and other stresses exhibit decreased sprouting (Vogt and Cox 1970, Powell and Tryon 1979, Johnson 1994b, Wilson and Kelty 1994).

Root carbohydrate content changes seasonally, with the highest levels occur-

Table 5. *Expected proportion of red oak stumps that will produce at least 1 codominant or better stem at stand age 20, with an 80% or better probability. (Average site quality - site index 18.3 m; adapted from Johnson 1975, Wendel 1975, Sander et al. 1984).*

	Proportion of stumps producing a competitive sprout in relation to tree age (years)			
DBH (cm)	40	60	80	100
5-13	0.86	0.86	0.49	0.49
15-28	0.86	0.86	0.46	0.46
30-41	0.86	0.86	0.38	0.38
43+	----	----	0.24	0.34

ring during the dormant season and the lowest levels following shoot expansion and leaf emergence in the spring. As a result, sprouting potential varies seasonally, and is lowest during the period following shoot expansion. Clearcutting upland oak species, including red oak, during the dormant winter months resulted in greater numbers and heights of stump sprouts than occurred with stumps of trees harvested during the growing season (Wendel 1975, Kays et al. 1985). This initial difference is short-lived, however, as the effects of differential root carbohydrate become less important to sprout size relative to microenvironmental effects on sprout photosynthetic capacity (Wendel 1975).

The height growth of reproduction that originate as sprouts is much greater than that of true seedlings, particularly after overstory release increases light availability (Liming and Johnston 1944, Wendel 1975, Smith 1980). This growth advantage is due, in part, to the existence of a large root system that is in physiological balance with the newly formed shoot. Stump sprouts have the further benefit of very large root systems with greater access to water and nutrients. The improved water status of oak sprouts during periods of reduced soil moisture as compared with intact plants can diminish the negative effects of water stress on photosynthesis (Kruger and Reich 1993, Castell et al. 1994).

Silvicultural prescriptions that enhance and exploit the sprouting potential of red oak seedlings and stumps should be a component of shelterwood systems. For example, mechanical scarification of a 2-year-old clearcut in Minnesota that broke off the stems of red oak reproduction and woody competition 15 cm above the soil surface doubled the number of subsequent oak stems compared with unscarified plots (Bundy et al. 1991). Because of the comparatively high fire resistance of oak, prescribed burning can be used to reduce the number of undesirable species while initiating the sprouting response (Swan 1970, Hannah 1987, Johnson 1994b). Mortality of overstory and understory species less resistant to fire also increases the amount of light available to oak sprouts (Johnson 1994b).

5.2 Artificial regeneration

Underplanting of red oak nursery stock can be used to supplement the amount of advance reproduction present in the understory (Johnson et al. 1986, Tworkoski et al. 1986, Gordon et al. 1995). Container-grown and bareroot red oak seedlings have been used for underplanting in the United States, but only bareroot stock is currently available in Ontario. The effective use of direct seeding as an artificial regeneration option in Ontario is uncertain, and protection of acorns from predation by herbivores may be required for this method to be successful (Auchmoody et al. 1993, Johnson 1994b). We therefore confine our discussion of artificial regeneration to planting, and concentrate primarily on the use of bareroot stock.

5.2.1 Nursery, handling and planting practices

A primary goal of forest tree nurseries should be to produce physiologically vigorous, well balanced seedlings with a capacity for rapid renewal of growth following planting (Dey and Buchanan 1995). High quality nursery stock can better withstand the cumulative negative impact of any activities from lifting through planting that decrease performance potential. Generally speaking, any cultural or environmental factor that increases the period between bud break and root regeneration will reduce seedling growth and initial field performance (Struve 1990).

The combined impact of seedling quality, and handling and planting practices on establishment and growth of oak seedlings is linked directly to the inherent growth characteristics of the species (section 3.0). Shoot growth after planting depends on carbohydrate reserves of the root and stem in hardwood seedlings, as they have no foliage at this time (Struve 1990). Nursery cultural conditions or damage to root systems during lifting, planting, etc. that reduce these energy reserves will therefore decrease shoot growth potential. Furthermore, root growth does not occur until after the spring shoot flush and depends on carbohydrates and growth regulators translocated from the newly formed shoot (Farmer 1975, Dickson et al. 1990). This entire developmental sequence must occur rapidly after outplanting for seedlings to re-establish root-soil contact and to assume a competitive growth rate.

5.2.2 Transplanting effects

Planting is often followed by a period of transplant shock, wherein growth and other physiological processes are inhibited. This occurs due to: (1) injury suffered during lifting, overwinter storage, handling, or planting, (2) poor initial hydraulic contact between roots and soil (Struve and Joly 1992) and/or (3) root-shoot ratios of nursery stock that are poorly adapted to the field environment. The physiological effects of transplant shock may be expressed for 3 to 4 years in clearcuts. In shelterwood environments, adverse effects may be suffered for a much shorter period provided that light levels are adequate to support new root growth (Crunkilton et al. 1992, Johnson 1994b).

The physiological effects of transplanting were demonstrated in a greenhouse study of root-pruned, transplanted and untransplanted red oak seedlings (Struve and Joly 1992). Root pruning was performed to simulate the root injury that results during stock lifting, handling and planting. Transplanted seedlings exhibited delayed bud break, a longer duration of the initial shoot flush, reduced total leaf area and leaf size, and comparatively slower growth. Root-pruning treatments that removed about 50% of root dry weight also reduced the water status of seedlings before the shoot lag phase (and the subsequent period of active root growth). Much less severe root pruning treatments have also been reported to decrease shoot growth and increase the likelihood of stem dieback (Larson 1975, Kaczmarek and Pope 1993).

Clipping of shoots (e.g., at 15 cm above the root collar) before planting has been tested as a potential means of reducing transplanting shock in red oak. This treatment stimulates sprouting from the root collar and the production of a shoot that is in better physiological balance with the planted root system. Shoot removal, however, reduces new root growth (Larson 1975, Johnson et al. 1984). This treatment may promote earlier recovery from transplant shock but results of field trials have not provided strong evidence of a long-term benefit to field performance (Johnson 1984, 1988; Johnson et al. 1984; Crunkilton et al. 1992; Kaczmarek and Pope 1993; Zaczek et al. 1993; Gordon et al. 1995). Shoot clipping treatments cannot yet be recommended.

5.2.3 Seedling characteristics and field performance

Observations that larger bareroot oak seedlings exhibit superior field performance has led to the general recommendation and perception that red oak planting stock should be as large as practical for handling and planting (Johnson et al. 1984, Zaczek et al. 1993). However, the initial shoot size of bareroot red oak seedlings has sometimes been reported as being poorly or negatively correlated with growth in the field (Olson and Hooper 1972, Thompson and Schultz 1995).

Seedling characteristics such as physiological vigor, root-shoot balance and other key morphological features may be better predictors of establishment and field performance than stem caliper. For example, seedlings with greater root branching and fibrosity have shown improved initial field performance (Johnson 1988, Thompson and Schultz 1995). Survival, height and diameter growth of bareroot red oak planted on a variety of old field and forested sites were generally higher for stock with more than 5 first-order lateral roots at the time of planting (Bardon and Countryman 1993, Teclaw and Isebrands 1993, Thompson and Schultz 1995). These roots provide the architectural framework of the root system, support the site of initiation of new roots and are active in water and nutrient uptake despite their woody, suberized character (Struve 1990).

5.2.4 Mycorrhizae

Mycorrhizae are composite root structures that form as a result of root infection by specialized groups of fungi. The symbiotic relationship provides the fungi with a food source (i.e., sugars) and a number of benefits to the host plant. Mycorrhizal red oak seedlings exhibit increased growth, enhanced water and nutrient uptake and reduced negative effects of allelopathic chemicals compared to nonmycorrhizal seedlings (Fisher and Cox 1978, Garrett et al. 1979, Hanson and Dixon 1987). The presence of mycorrhizal roots also improves drought tolerance and protects fine roots from disease (Perry et al. 1987, Kropp and Langlois 1990).

Roots may become infected by many different fungal species but the benefits of this symbiosis are greatest when tree species are matched to the fungal species with which they are naturally associated. Although bareroot red oak seedlings are infected by mycorrhizae in the nursery, fungal species in nursery soils differ from those in forest soils. Fungi indigenous to forests begin colonizing oak roots the first year after planting, and slowly replace the mycorrhizae from the nursery (Garrett et al. 1979). The effect of infection of red oak nursery stock by symbionts other than the "preferred" natural species is unknown.

Cultural practices that inhibit mycorrhizal development (i.e., soil fumigation, etc.) or result in loss of mycorrhizal roots (i.e., lifting, planting, etc.), temporarily reduce the growth potential of planted seedlings. Silvicultural practices can also decrease fungal populations in the field and, therefore, infection with naturally occurring species after planting (Kropp and Langlois 1990). The type of mycorrhizal species that are symbiotic with the oaks (i.e., ectomycorrhizae) cannot survive for extended periods in the absence of vigorous roots of a living host. Mycorrhizal populations are generally low in large clearcuts, particularly where logging slash has been burned, and in old cutovers (Harvey et al. 1980a,b). It seems likely that the presence of a residual stand in shelterwood systems would serve to retain a viable source of native mycorrhizal fungi for root infection of underplanted red oak seedlings.

5.2.5 Container stock

Red oak container stock is being produced elsewhere in North America and has been used effectively in artificial regeneration efforts. Container stock, although initially smaller than bareroot stock in most cases, often exhibits greater height growth 2 to 3 years after planting (Teclaw and Isebrands 1993, Zaczek et al. 1993). The initiation of root growth after removal from cold storage was reported to be more rapid in container stock than bareroot (Johnson et al. 1984). The prompt renewal of root growth by container stock after planting was associated with enhanced rates of shoot elongation and leaf area production. Protection of container seedling root systems and their carbohydrate reserves from damage during handling and planting is also probably related to the rapid growth resumption observed.

The more vigorous, relatively undisturbed root systems of container seedlings may also improve water and nutrient relations after planting. One-year-old red oak container stock planted in a clearcut and under a partially thinned stand exhibited enhanced water status the first 2 years after planting compared with 2+0 bareroot stock (Crunkilton et al. 1992). Excavation of the seedlings after year 2 revealed that bareroot seedlings had less total root length than container seedlings, a feature likely related to their poor water relations. Although container stock exhibits many desirable features, the cost of producing this stock may outweigh the benefits of its use over large bareroot seedlings (Johnson 1984, Zaczek et al. 1993).

6.0 Management by shelterwood

Shelterwood cuts should be designed to further the development of advance reproduction by regulating light levels at the forest floor (Loftis 1990b). Foresters can vary the intensity, number and frequency of shelterwood harvests to develop oak advance reproduction without promoting understory competition. For the successful development of oak under a shelterwood, it is essential to control understory vegetation, especially on productive sites where undesirable species compete with oak (Sander 1979; Loftis 1983, 1985; Johnson et al. 1989; Lorimer 1989; Pubanz and Lorimer 1992).

Where oak advance reproduction is present, but not large, or when oak is underplanted, a 2-cut shelterwood is recommended (Gottschalk 1983, Johnson et al. 1986). The initial harvest creates the shelterwood, provides additional light to the forest floor and promotes the development of oak advance reproduction. It is often done in combination with a vegetation control treatment (section 6.2). The final harvest releases the oak advance reproduction. In natural regeneration prescriptions, a 3-cut shelterwood may be used when oak advance reproduction is sparse. In this situation, the first thinning is a seed-cut to increase the crown exposure of the good acorn producers (Dey 1995). Once the oak is established, the shelterwood is created.

6.1 Residual overstory

Recommendations for shelterwoods are often defined using basal area, stocking, or crown cover. This can make the interpretation and comparison of shelterwood prescriptions difficult. Although crown cover is a better indicator of understory light conditions, basal area and stocking level are most commonly used to regulate stand density. However, basal area and stocking level are not closely correlated with crown cover and thus do not provide a direct measure of light intensities at the forest floor (Sloan and Zastrow 1985).

Figure 20. *The initial shelterwood cut produces a high, uniform residual canopy by harvesting trees "from below".*

6.1.1 Residual crown cover

Most shelterwood prescriptions call for a high, uniform canopy obtained by thinning from below (Figure 20) (Sander 1979, Jacobs and Wray 1992). Initial shelterwood treatments should emphasize the removal of subcanopy trees and woody stems in conjunction with prescribed overstory reductions (Figure 21)

Figure 21. *During the first shelterwood harvest, the taller subcanopy trees should be removed to increase light levels at the forest floor and to reduce competition for soil moisture. The stumps of cut stems can be treated with herbicides during harvesting to reduce sprouting of undesirable species.*

(Sander 1979; Loftis 1983, 1990b; Lorimer et al. 1994). Retention of full-crowned oaks in codominant or dominant crown classes provides high shade to inhibit understory competition. In addition, leaving these oaks ensures optimum acorn production in years of good seed crops and therefore promotes adequate regeneration (section 5.1.2).

When understory vegetation is abundant, residual crown cover after the first shelterwood cut should be at least 70% (Arend and Scholz 1969, Lorimer 1989). Under the same conditions, a cut that leaves only 30 to 50% crown cover may result in severe understory competition (Sander 1979, Loftis 1983). If understory vegetation is sparse, however, or has been reduced effectively by vegetation management treatments, overstory crown cover can be reduced to 50% in the initial harvest (Arend and Scholz 1969, Wolf 1988). In some cases, a lighter shelterwood cut (leaving 85% crown cover) combined with the removal of understory trees may also improve the survival and growth of oak seedlings (Pubanz and Lorimer 1992, Lorimer et al. 1994).

6.1.2 Residual density and stocking

As site quality increases, a more dense residual overstory is required to prevent the release of undesirable vegetation (Loftis 1990b, Schlesinger et al. 1993). When red oak reproduction is present, Loftis (1990b) recommends reducing overstory basal area by 30 to 40% on high quality sites (those with oak site indices ranging from 21 to 27 m), especially when aggressive intolerant species (e.g., poplars) are present. The relatively dense shelterwood canopy limits the establishment and growth of shade intolerant species (Loftis 1990b). Hill and Dickmann (1988) report that on good quality sites, where shade tolerant species such as sugar maple are the major competitors, greater reductions in the initial stand basal area (i.e., 4.8 to 8.0 m^2/ha residual basal area) can be made in the initial shelterwood harvest. Stocking of shade tolerant reproduction is reduced as the amount of overstory removal increases on good sites. However, post-harvest control of competing vegetation may be necessary to maintain the long-term dominance of oak in the upper crown classes.

A shelterwood study was established near Foymount, Ontario in a red oak dominated stand that averaged 31

m^2/ha of basal area (trees >10 cm in dbh) before harvest (section 4.7). Light (7.3 m^2/ha residual basal area) and moderate (17.7 m^2/ha) shelterwoods were created by harvesting from below. Both shelterwood treatments resulted in similar microenvironments (Figure 9) that enhanced P_n of red oak compared to that of red oak growing in the understory of uncut stands (Figure 10). In northern hardwood stands, researchers have found that a residual overstory density of 9 to 12 m^2/ha provides sufficient light (45% of full sunlight) for acceptable growth of mid-tolerant species (Godman and Tubbs 1973, Leak and Tubbs 1983, Kelty 1987).

If oak advance reproduction is absent, Jacobs and Wray (1992) recommend leaving 70% stocking (18 to 32 m^2/ha). When oak advance reproduction is present, overstory density can be reduced to 60% stocking (according to Gingrich (1967)) (Graney and Rogerson 1985, Sander 1988, Jacobs and Wray 1992). Although 40% stocking is associated with light levels needed for maximum seedling shoot growth and photosynthetic rates in red oak (30 to 50% of full sunlight), there is a tradeoff between providing enough light for maximum oak growth and limiting the release of understory competition (Hannah 1988).

Sander (1979) recommends that the first shelterwood cut leave 60% stocking, the minimum stocking for full site utilization, to help control development of the understory. Schlesinger et al. (1993) found that removing all non-oak stems ≤4 cm in dbh and reducing the overstory to 60% stocking(according to Gingrich (1967)) minimized understory competition on good quality sites. On average quality sites, they found that the reduction of understory competition had little effect on oak advance reproduction, and that reduction of the overstory to 40% stocking resulted in the greatest amount of large oak advance reproduction. Several stocking charts have been developed to help foresters regulate stand density in: (1) Central States oak-hickory forests (Gingrich 1967), (2) New England red oak forests (Sampson et al. 1983) and (3) Wisconsin red oak forests (Figure 22) (McGill et al. 1991).

6.2 Control of understory vegetation

Control of understory vegetation is necessary when competition is expected to be a problem following shelterwood harvesting (Ehrenfeld 1980, McGee 1984).

Jacobs and Wray (1992) propose a method for evaluating the severity of understory competition. Several 6-m^2 circular plots are used to inventory understory vegetation. If 30% of the plots are dominated by competing species and oak reproduction is less than 30 cm in height, then understory control is recommended. When oak regeneration in the plots is primarily larger advance reproduction and stump sprouts, then understory control measures are necessary only when 70% of the plots are dominated by undesirable species.

Establishment of red oak will be enhanced when understory competition is reduced because seedlings and new sprouts are capable of rapid height growth when moisture and light are not limiting (Farmer 1975). Herbicides, mechanical scarification, and prescribed fire are recommended for controlling vegetation in the understory (Scholz 1959, Johnson and Jacobs 1981, Nyland et al. 1982, Gottschalk 1983, Lorimer 1985, Van Lear and Waldrop 1988).

6.2.1 Herbicides

Herbicide application to control understory trees taller than 1.5 m or

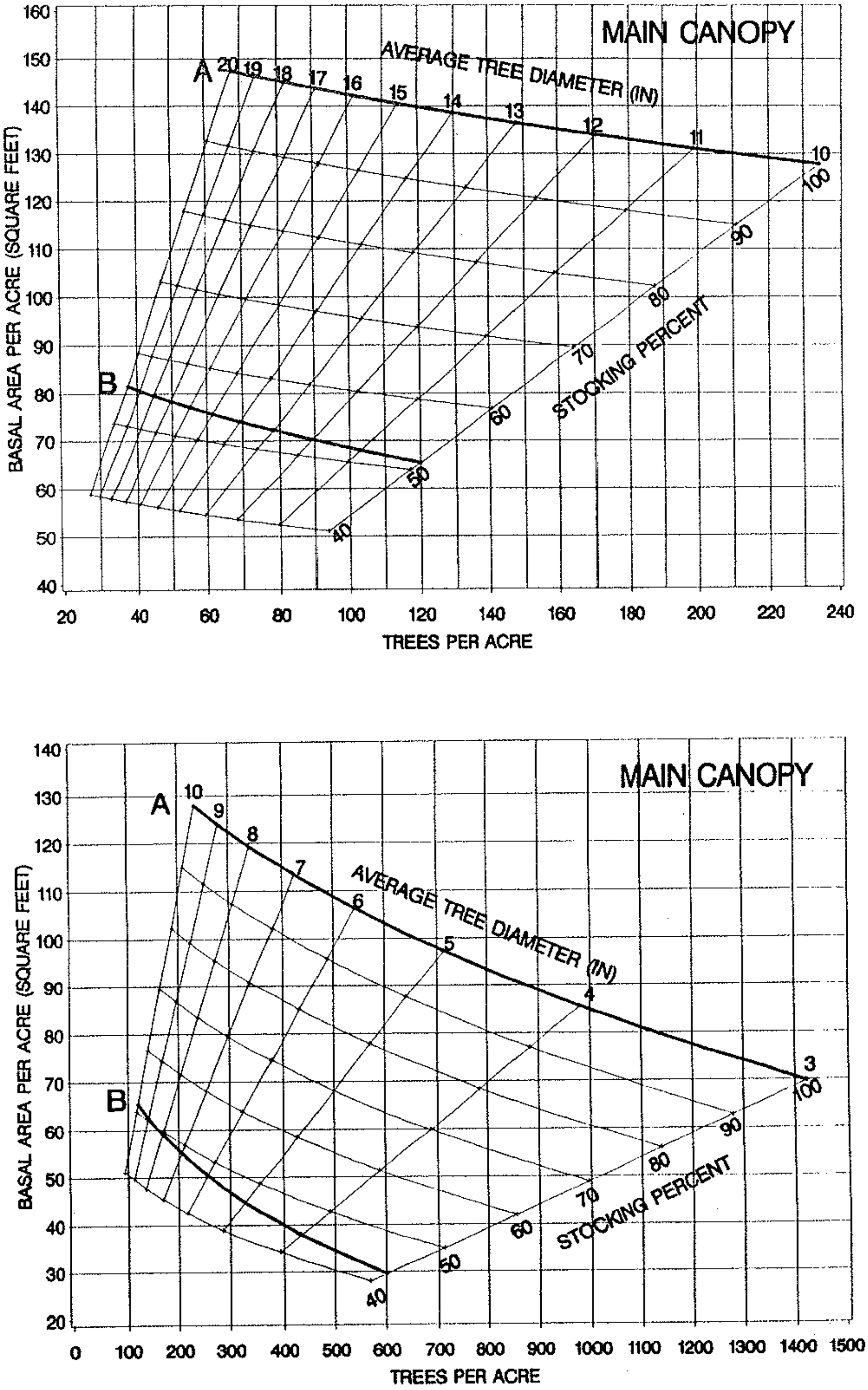

Figure 22. *Stocking chart for red oak in Wisconsin (from McGill et al. 1991). Stand stocking is determined from an inventory of all main canopy trees in the dominant, codominant and intermediate crown classes that are greater than or equal to 5 cm in dbh.*

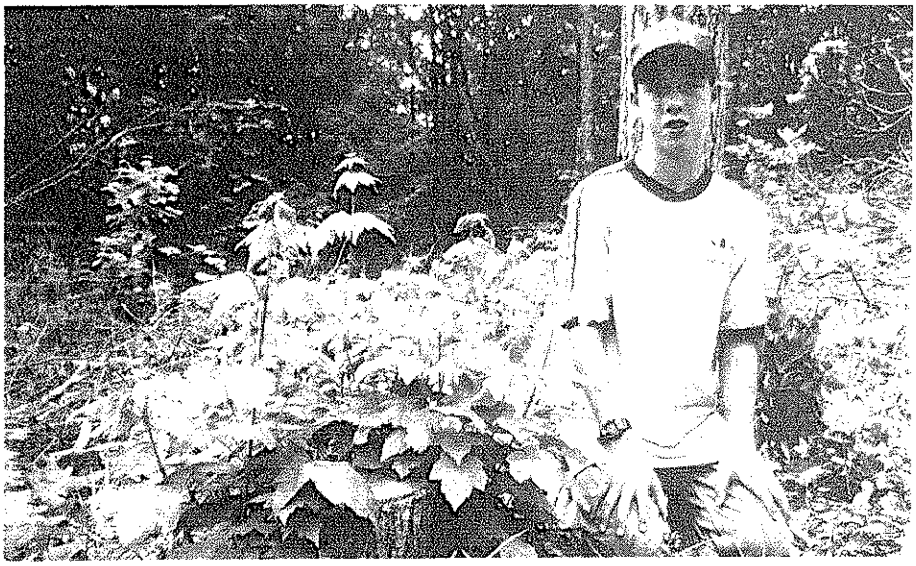

Figure 23. *Cut stems of many undesirable species, such as this red maple, sprout prolifically. These sprouts grow rapidly in the more open environment of a shelterwood and compete with oak reproduction.*

larger than 1.5 cm in dbh has proven beneficial to the establishment, survival and growth of both natural and underplanted red oak and upland oaks (Johnson et al. 1986, Loftis 1990b, Schlesinger et al. 1993, Lorimer et al. 1994). Herbicides (e.g., glyphosate) can be applied by tree injection, by basal or foliar spraying, or to the cut stumps of the taller competing understory and subcanopy trees. Application to stumps is done at the time of cutting, regardless of season. Cutting stems alone has not been effective in reducing competition, especially on higher quality sites, because many of the trees produce sprouts, which grow rapidly in the open (Figure 23). Basal spraying and tree injection can be done any time of the year. Basal spraying is especially effective and easy to apply on trees less than 2.5 cm in dbh or when there are dense clumps of small diameter trees. Foliar sprays are applied during the growing season (August to September), but efforts must be made to protect the oak reproduction. This can be accomplished by directed spraying or by cutting the oak reproduction before herbicide application to competition. The oaks will subsequently sprout and should grow well with less competition.

Red oak has been successfully regenerated without large advance reproduction present before overstory removal (Johnson and Jacobs 1981, Crow 1992). Johnson et al. (1989) reported that oak regeneration comprised one-third of the basal area in a Wisconsin clearcut 11 years after harvest. The understory had been controlled, however, with several preharvest applications of herbicide. The first herbicide application was done 2 years before clearcutting and the second occurred just before harvesting. A bumper acorn crop in the fall before the harvest set the stage for abundant new red oak seedlings.

6.2.2 Prescribed burning

Prescribed burning has long been recommended as a method for controlling competition and enhancing oak regeneration (Figure 24) (Lorimer 1993, Schlesinger et al. 1993, Lorimer et al. 1994). Fire may also be effective in reducing habitat for small mammals and thus would be a useful site preparation treatment in direct seeding operations (Dey and Buchanan 1995). It has also been reported that burning may reduce populations of acorn insect predators

Figure 24. *Prescribed burning is recommended for controlling understory competition and favoring red oak regeneration. Most burns in Ontario are conducted in the spring before leaf-out.*

such as weevils (section 5.1.3) (Wright 1986, Galford et al. 1988).

Burning is often conducted in the spring, before leaf flushing has begun on a majority of the vegetation. Single fires are ineffective in reducing the amount of competition because many undesirable woody species that experience shoot-kill will produce sprouts (Figure 25) (Loftis 1990b). Repeated fires are required to reduce competition.

Although the ideal number and frequency of prescribed fires for oak regeneration is currently unknown, the results of prescribed burning and fire history studies indicate that burning every 3 to 5 years favors oak regeneration. Nyland et al. (1982) recommended that prescribed burning be done every 2 to 3 years to promote oak regeneration. Near Papineau Lake, Ontario, Guyette and Dey (1995) found that fires had burned every 5 years from 1880 to 1920 on a ridgetop site that is now dominated by mature red oak. More frequent burning in shelterwoods has not benefited oak reproduction. Three consecutive annual burns in a Bracebridge oak shelterwood (70% residual crown cover)

Figure 25. *A single preharvest spring fire killed the aerial portion of this 10.6-cm dbh sugar maple sapling. Two years after the fire, a dense sprout clump was developing under a heavy overstory canopy. Repeated burning is required to reduce understory competition and favor red oak regeneration.*

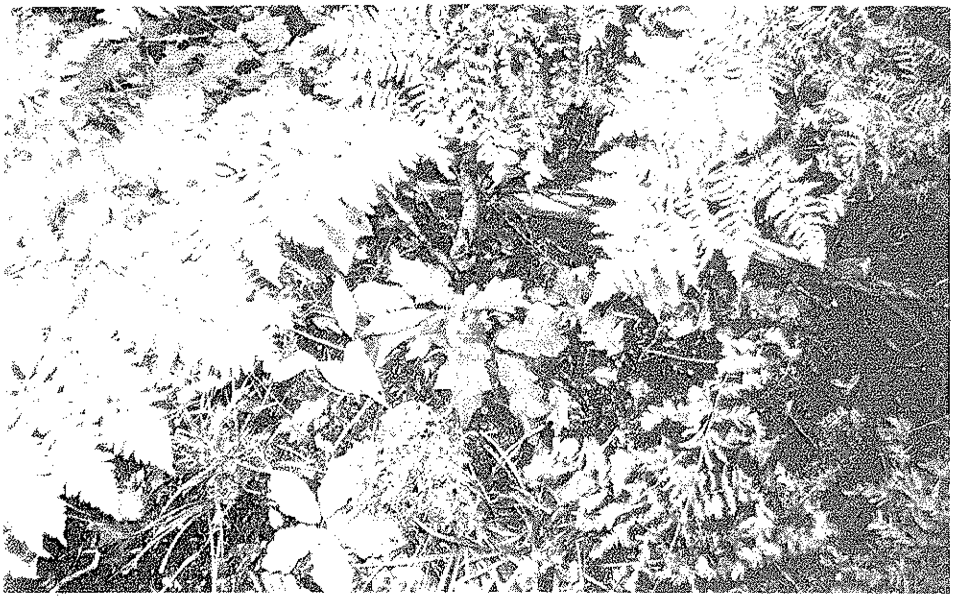

Figure 26. *Three consecutive spring burns in a Bracebridge red oak shelterwood reduced understory woody vegetation but promoted bracken fern. Most oak reproduction is small and lies beneath the bracken fern canopy.*

have effectively reduced the amount of understory woody vegetation but have also promoted the dominance of bracken fern and adversely affected the red oak advance reproduction (Mutchmor, pers. comm.) (Figure 26).

Fire-caused mortality of red oak varies with seedling age. Both Johnson (1974) and Mutchmor (pers. comm.) have found that prescribed burning in the spring caused 60 to 70% mortality of 1-year-old red oak seedlings. However, mortality was only 30% for seedlings that were at least 3 years old. Spring fires also caused significant reductions in acorn viability (Auchmoody and Smith 1993; Dey, unpubl.). When stands have produced good to bumper acorn crops, understory burning should be delayed for up to 3 years to allow sufficient time for germination and seedling establishment.

6.2.3 Scarification

Mechanical scarification can also be used to control competing understory vegetation by shearing off the stems of woody vegetation and uprooting individuals (Bundy et al. 1991, Jacobs and Wray 1992). Obviously, existing oak advance reproduction are also subject to damage, but oak will produce sprouts if their root systems remain intact. Scarification in conjunction with a good acorn crop can increase the number of oak seedlings that initially become established (Scholz 1955; Johnson 1994b; Dey, pers. observ.) because acorns may be forced into mineral soil, which protects them from desiccation and reduces predation (Galford et al. 1991). Scarification before direct seeding may also improve oak establishment by destroying habitat for small mammals (Dey and Buchanan 1995). However, scarification operations should not displace or remove the upper soil horizons. A mixing of leaf litter, humus and mineral soil provides ideal seedbed conditions for red oak and a variety of other desirable tree species. Steep terrain or areas with numerous rock outcrops may limit the use of scarification.

6.3 Stocking targets

6.3.1 Advance reproduction

The status of oak advance reproduction can be used to time additional shelterwood cuts or to plan the final overstory removal. Sander (1979) suggests that when oak advance reproduction is about 0.9 m tall, overstory stocking can be reduced to 50% (according to Gingrich (1967)). Final overstory removal is recommended for central Pennsylvania oak stands when 70% of 4-m^2 plots contain at least one desirable oak that is greater than 0.6 m tall (Figure 27) (Wolf 1988). For the upland oak forests of the midwestern United States, adequate oak advance reproduction is a minimum of 1.4 m tall, or 13 mm in diameter at ground level (Clark and Watt 1971; Sander 1971, 1972; Sander et al. 1976). Stems of this size or larger are most likely to produce reproduction in the codominant or dominant crown classes (Sander et al. 1984). Approximately 1,075 stems per ha are needed to produce a pole stand that contains 30% oak by basal area (Sander et al. 1976). Others contend that from 1,000 to 10,000 oak advance reproduction per ha are needed to ensure adequate regeneration (Clark and Watt 1971).

The actual number of oak advance reproduction needed for regeneration depends on the preharvest size of the reproduction, the desired level of oak stocking, the site quality, the management intensity, and varies among ecosystems. In general, higher stocking and larger stems of oak advance reproduction are needed as: (1) site quality increases, (2) competition increases, (3) management intensity decreases and (4) the desired level of oak stocking increases. Smaller stems of oak advance reproduction may have lower developmental potential, but with sufficient numbers, oak regeneration may still be successful. However, there are numerous examples of oak regeneration failures despite abundant small advance reproduction (McGee and Hooper 1975, Rudolph and Lemmien 1976, Standiford and Fischer 1980, Loftis 1983, Beck and Hooper 1986, Hix 1988).

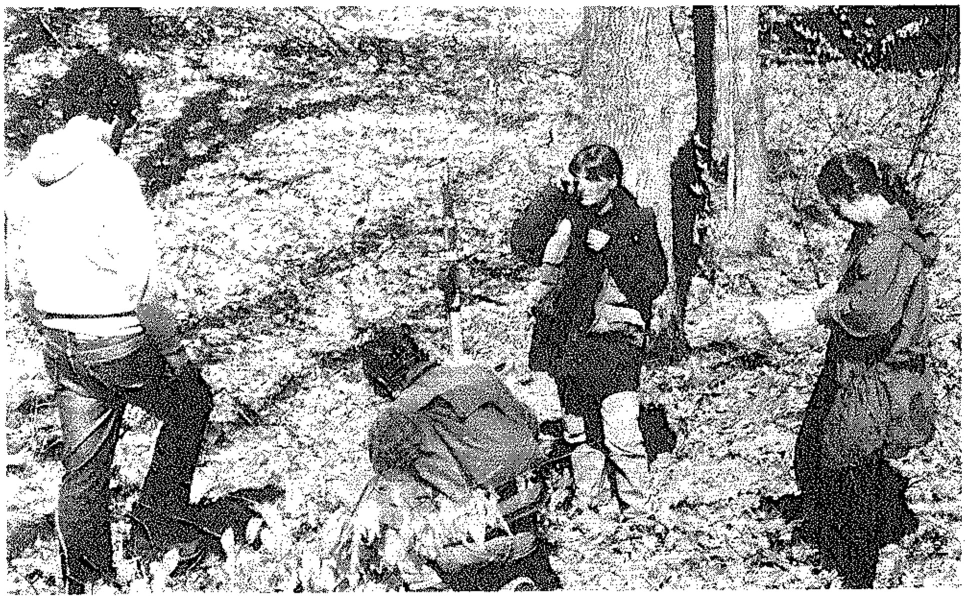

Figure 27. *Preharvest inventories of the understory and overstory are used to evaluate the oak regeneration potential. This information is necessary for developing silvicultural prescriptions for red oak regeneration.*

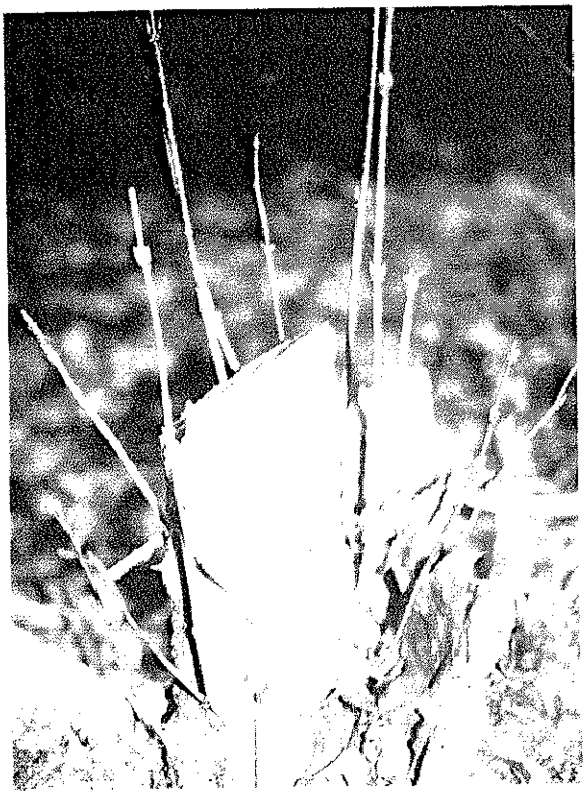

Figure 28. *Sugar maple stems cut during harvesting will sprout prolifically, especially from stems that are less than 15 cm in diameter. The capacity to produce vigorous sprouts declines with increasing tree age and diameter.*

In the Central Hardwood Region, Sander et al. (1984) provide a method for evaluating the regeneration potential of upland oak stands using preharvest inventories of the overstory and advance reproduction (Figure 27). Comparable preharvest guidelines for assessing oak regeneration potential are being developed for Ontario.

6.3.2 Stump sprouts

Where oak stump sprouts are expected after a harvest, they can be used to compensate for deficiencies in the amount of oak advance reproduction. As few as 75 to 100 clumps of red oak stump sprouts per ha can comprise one-third of the stand basal area by age 23 (Johnson 1975). However, not all red oak overstory trees will produce sprouts after harvesting (section 5.1.6). Under a shelterwood, unmerchantable oaks may act as a source of stump sprouts if they are not harvested until the final overstory removal. They can be left as a part of the shelterwood to help provide shade for the control of understory competition. In addition, they may contribute to the supply of acorns.

Overstory stems of non-oaks and larger shade tolerant saplings will also produce sprouts when they are cut. Because stump sprouts represent the fastest growing form of reproduction, non-oak sprouts are serious competitors. Sugar maple stumps sprout prolifically, with more than 90% of the trees ≤15 cm in diameter producing sprouts (Figure 28) (Church 1960, Wendel 1975). However, the number of sugar maple sprouts decreases rapidly as stump diameters increase beyond 15 cm (Solomon and Blum 1967). The abundance of red maple stump sprouts increases with increasing stump diameter up to 23 cm, beyond which it declines (Solomon and Blum 1967). Competition from non-oak sprouts can be minimized by treating stumps with herbicides (e.g., glyphosate) at the time of harvesting.

Sprouting also occurs when large advance regeneration is damaged by logging or by sudden exposure to full sunlight after harvest. New sprouts are desirable because of their rapid growth rates and good stem form (Ward 1966, Wendel and Trimble 1968, Sander 1971, Sander and Clark 1971, Loftis 1990a). Recovery from shoot dieback is rapid and the sprouts are generally as tall as undamaged reproduction within 10 years (Jacobs 1974, McQuilkin 1975, Kelty and Nyland 1981).

6.3.3 Underplanting red oak

When the number of oak advance reproduction and stump sprouts are insufficient to meet desired levels of oak regeneration, underplanting oak in a shelterwood can be used to supplement natural regeneration. The sequence of treatments for a shelterwood prescription to regenerate red oak by underplanting is as follows (Johnson et al. 1986):

1. Reduce the competition from woody plants $\leq$5 cm in dbh by applying herbicides before planting. Protect any existing oak advance reproduction.
2. Create a uniform shelterwood (55 to 65% residual stocking) by harvesting from below. Treat the stumps of undesirable species with herbicides. Removal of the taller woody subcanopy, such as shade tolerant saplings of sugar maple, ironwood (*Ostrya virginiana* [Mill.] K. Koch) and beech, is important.
3. Underplant large red oak stock ($\geq$10 mm in diameter 2 cm above the root collar). Plant from 2.4 to 4.3 seedlings of this size to obtain 1 successful tree.
4. After 3 growing seasons, remove the shelterwood. Treat the stumps of undesirable species with herbicides when they are cut. The final harvest should be based on a preharvest survey of the advance reproduction and a consideration of the contribution of stump sprouts to the regeneration potential for oak. Harvesting should be delayed if the oak regeneration potential is inadequate.
5. Repeat the herbicide treatment in step 1 if needed at the time of overstory removal, ensuring that the oaks are protected by using directed spraying or by shoot clipping the oaks before herbicide application.

6.4 Final overstory removal

Final overstory removal should be delayed if the status of oak advance reproduction and sprouting potential of the overstory indicates that future oak stocking will not meet management objectives. However, once adequate numbers of sufficiently large red oak advance reproduction are established, they should be released from the shelterwood. Delaying the final overstory removal inhibits oak reproduction and favors the shade tolerantspecies.

In the final overstory harvest, it is not necessary nor always desirable to remove the entire shelterwood. Retention of the best acorn producing oaks until the new stand reaches reproductive maturity (about 50 years) provides a sustainable supply of acorns for wildlife species. In addition, maintenance of a high forest canopy may provide aesthetic benefits in areas where visual quality is a concern. A light overstory (e.g., 30 to 37 codominant trees per ha; 4.0 to 5.9 m^2/ha) will not have long-term adverse effects on the development of hardwood reproduction (Miller and Schuler 1995). However, it is important that undesirable trees $\geq$2.5 cm in dbh be felled during harvest because otherwise, they can inhibit the growth of desirable reproduction.

Ensuring that a certain portion of oaks in the previous stand survives into the next generation will more closely mimic *natural* stand processes. In mature upland oak forests in central Ontario, many of the oaks are nearly the same age, often in the range of 80 to 120 years.

However, there is a small proportion of oaks that may be 180 years or older (Guyette and Dey 1995). Shelterwood systems can be modified to produce relatively even-aged stands that retain structural elements characteristic of stands formed by natural processes.

7.0 Summary

Red oak is a valuable species in the Great Lakes-St. Lawrence forests of Ontario, providing economic, habitat, aesthetic and biodiversity values. Traditional harvesting methods used in Ontario fail to regenerate oak in sufficient quantities to maintain the current level of oak growing stock, and forests are increasingly succeeding to shade tolerant species such as sugar maple. The present red oak forests originated during a period characterized by frequent disturbances. Now, fire suppression and selection harvesting are creating environments that favor the regeneration and dominance of shade tolerant species.

Red oak is a stress tolerant species that is more drought tolerant than its associates. It exhibits conservative growth habits such as preferentially storing carbohydrates in its root system rather than allocating them to shoot growth. The sprouting response to shoot dieback caused by stress (e.g., drought) or disturbance (e.g., fire) is well developed in red oak.

The regeneration strategy of oak gives it a competitive edge on lower quality, drier sites or where ecosystem disturbances are frequent. On better quality sites, it competes less effectively with shade tolerant species where the formation of small canopy gaps is the predominant disturbance mechanism. Oak seedlings with relatively small root systems are unable to take full advantage of sudden increases in resources (e.g., light, water and nutrients) that occur following major stand disturbances such as clearcutting or severe fires. In these environments, early-successional pioneer species such as white birch, pin cherry and poplar dominate.

Growth of the intermediate shade tolerant red oak increases with increasing light levels up to about 50 to 70% of full sunlight. Although oak seedlings need only 2 to 5% of full sunlight to meet their basic respirational demands, little new growth occurs in heavy shade. Red oak requires a minimum of 20% of full sunlight before any new shoot growth occurs. Light levels in undisturbed, closed canopied Ontario hardwood stands typically range from 1 to 10% of full sunlight.

Oak advance reproduction growing in heavy shade have low root energy reserves and reduced potential for sprouting following shoot dieback. Heavily suppressed seedlings are also less able to tolerate environmental and biotic stresses and mortality is high. Numerous oak seedlings may be present following bumper acorn crops, but advance reproduction does not accumulate in the understory, especially on high quality sites. Seedlings that do survive are often small (e.g., <15 cm tall) and are unable to compete with larger, shade tolerant advance reproduction or shade intolerant species when released by overstory harvesting.

Many insect, bird and mammal species feed on acorns and oak seedlings. In years of low-to-average acorn production, the majority of acorns and new germinants are damaged or consumed. Oak reproduction becomes established in large numbers primarily in years of heavy acorn production. However, even in bumper crop years, desiccation of seed before or during germination can cause a substantial loss of the seed crop.

Acorns are recalcitrant, and they must maintain a relatively high moisture content (e.g., >30%) to remain viable. Acorns buried in 2 to 5 cm of mineral soil or beneath leaf litter are less likely to desiccate in the spring. Seed buried in mineral soil may also be less susceptible to predation than seed in the litter layer. Burial in the soil improves germination. New oak germinants can grow well the first year even in a shaded understory. Carbohydrate reserves in the relatively large acorn support this initial seedling growth, but after the acorn reserves are exhausted, oaks need sufficient light for continued growth.

Competition with other plants for limited resources is a major factor that regulates the development of oak reproduction. On good sites, light is probably the most limiting environmental resource, whereas soil moisture and nutrients become more limiting on poor sites. Controlling competition in both the overstory and the understory is necessary to provide adequate resources for the growth and survival of oak reproduction. Reducing overstory competition alone through partial cutting has not been effective in promoting the development of oak reproduction. Thinning the overstory when there is a dense understory does little to increase light at the forest floor and promotes the development of shade tolerant advance reproduction. Reducing overstory and understory competition together should produce adequate light levels (35 to 65% of full sunlight) at the forest floor for maximum oak seedling development.

Red oak has the ability to sprout after shoot dieback or stem removal. Stump sprouting capacity increases with stem diameter up to a threshold, beyond which it decreases. The ability to produce sprouts also declines as trees age. Oaks less than 80 years old are good sprouters. Oak sprouts that originate from below the ground produce high quality mature trees.

Oak seedlings usually sprout after stress- or disturbance-induced shoot mortality. The growth rate of sprouts is largely controlled by the size of the parent root system. In the understory, seedlings gradually increase their root mass provided that there is sufficient light at the forest floor. Relatively large root systems are able to support rapid sprout growth following overstory removal, allowing oaks to compete with other reproduction. When the overstory is removed, new oak seedlings or advance reproduction with small root systems are quickly over-topped by intolerant species and by larger shade tolerant advance reproduction.

The shelterwood system is often recommended for oak regeneration. A partial overstory canopy moderates the microclimate at the forest floor, improving conditions for germination and seedling establishment. Shelterwood overstories reduce the diurnal amplitude of air and soil temperatures as well as their extremes, moderate seedling water use and decrease the amount of frost injury. Overstory thinning also increases the amount of light at the forest floor, especially when done in conjunction with controlling understory vegetation.

Shelterwood harvests can be used to increase the acorn production potential of a stand. Acorn production is primarily under genetic control but is also related to age, diameter and crown characteristics. Some oaks are consistently good acornproducers, whereas others produce poorly. Oaks older than 50 years can produce good acorn crops, and bumper seed crops occur every 3 to 5 years. Acorn production increases as tree diameter increases up to 50 cm in dbh. Trees with large, full crowns exposed to direct sunlight can produce substantially more acorns than the small, shaded crowns of oaks in the lower crown classes. Overstory thinning can be used to release known good seed producers in the codominant and dominant crown classes. Leaving seed producing oaks throughout the residual overstory also improves dispersal of acorns.

When artificial regeneration is required to supplement natural oak reproduction, underplanting shelterwoods is the recommended approach. Shelterwoods provide a less stressful seedling environment by reducing wind speed, increasing relative humidity and moderating temperature. The length of the transplanting shock period may be reduced under a shelterwood. In addition, the shade of a partial overstory can suppress the growth of competing species.

The first shelterwood harvest should create a high, uniform overstory canopy by thinning from below. About 70% crown cover or 60% stocking should be retained after the initial harvest. On higher quality sites, where understory competition is present, higher levels of crown cover or overstory stocking may be needed to control the release of competing species. Where understory competition is sparse or has been controlled, residual crown cover or stocking can be reduced to 50%.

Well developed subcanopies of shade tolerant vegetation should be controlled before or at the time of the initial shelterwood harvest. Thinning the overstory without understory vegetation management will not greatly improve conditions for the development of oak advance reproduction. The shade tolerant understory vegetation will be released, and may suppress any oak reproduction. Herbicides, prescribed burning or mechanical scarification can be used before or after harvesting to control competing vegetation.

The first shelterwood harvest should be delayed if oak advance reproduction is sparse or absent, unless artificial regeneration by underplanting is prescribed. When relying on natural oak reproduction, a preharvest survey of the understory and overstory can be used to time the initial harvest. Delaying harvesting until natural oak reproduction is established is necessary because it is difficult to predict acorn crops.

Large ($\geq$10 mm in diameter 2 cm above the root collar) bareroot red oak nursery stock with 5 or more permanent first-order lateral roots should be used for underplanting in shelterwoods. Approximately 2 to 4 seedlings of this size must be planted to produce 1 successful stem of oak reproduction. Planting should occur after understory vegetation control and shelterwood harvesting are completed. Final overstory removal should be considered 3 growing seasons after underplanting.

Additional overstory harvests should be timed to release oak advance reproduction when they are sufficiently large and abundant. A light residual basal area (4.0 to 5.9 m^2/ha) in codominant or dominant trees can be retained for extended periods of time without inhibiting reproduction. Leaving a few good seed bearing oaks can sustain the supply of acorns for wildlife while the new stand is maturing. The final harvest should be delayed if the oak regeneration potential is inadequate, and this decision should be based on preharvest surveys.

Unfortunately, no guidelines exist for assessing the regeneration potential of red oak forests in Ontario. Inventory and evaluation methods have been developed for other red oak ecosystems in the United States and these have been presented in this report. The adequacy of oak advance reproduction and stump sprout potential will vary among ecosystems, and in response to management intensity and objectives. Studies are underway in Ontario to define reproduction standards for red oak and its associates, but until quantitative guidelines are developed, professional judgement must prevail. Post-harvest vegetation management may also be necessary to maintain the dominance of red oak reproduction at desired levels.

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