Chapter 8: The Role of Young, Recently Disturbed Upland Hardwood Forest as High Quality Food Patches

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Abstract Young (1–10 yr post-disturbance) upland hardwood forests function as high-quality food patches by providing abundant fruit, and nutritious foliage and flowers that attract pollinating and foliar arthropods and support high populations of small mammals that, in turn, are prey for numerous vertebrate predators. Reductions in basal area increase light penetration to the forest floor, which stimulates vegetative growth and promotes fruiting. Fruit biomass (dry edible pulp) can be 5 to nearly 50 times greater in young forest than mature forest as "pioneer" species, such as pokeweed and blackberry, ericaceous shrubs, various forbs and grasses, and stump sprouts of many tree species produce fruit. Forage production (dry kg/ha) can increase substantially after disturbances that significantly reduce overstory basal area, such as timber harvests, heavy thinning, or intense prescribed fire. Hard mast (nut) production can be sustained in young forests if some mature, good mast-producing oak, hickory, or beech trees are retained. Balancing the creation of young, recently disturbed upland hardwood forests with the desired amount and distribution of other forest age-classes will sustain high-quality food patches for wildlife within a landscape context.

8.1 Introduction

Deciduous forest of the Central Hardwood Region is a patchwork of stand ages and structures that result from natural small-scale disturbance, such as death of individual trees, and larger-scale events, including fire, ice, wind, and insect outbreaks (White et al. Chapter 3). Many forest management activities, such as timber harvest, thinning, and controlled burning, also create disturbances. Varied types and intensities of disturbances result in an assortment of structural features that complicate a simple definition of young upland hardwood forest. Yet, all share similar attributes, including a well-developed groundcover or shrub and young tree component, and absence of or discontinuous mature tree canopy (Greenberg et al. Chapter 1).

Abundant light and reduced competition created by reductions in overstory tree density coupled with soil perturbation and scarification from disturbances promote germination, foliar growth, flowering, and fruiting by many plant species on the forest floor. Disturbance also promotes colonization by disturbance-adapted plants, such as blackberry (*Rubus* spp.) and pokeweed (*Phytolacca americana*), that produce prodigious amounts of fruit (Greenberg et al. 2007). Open, recently disturbed forests provide an abundance of native fruits, woody browse, nutritious foliage and flowers that attract arthropods, and high densities of small mammals that serve as prey for numerous snake, bird, and mammalian predators. Thus, these young forests function as high-quality food patches for many wildlife species. The important role of young hardwood forests in supporting wildlife is becoming increasingly recognized by natural resource professionals. In this chapter, we synthesize results of our own research and other studies on fleshy fruit, hard mast, browse, and arthropod and small mammal (as prey) production in young (less than 10 years post-disturbance) upland hardwood forests of the Central Hardwood Region of the USA (see Fig. 1.1).

8.2 Fleshy Fruit

Fleshy fruit (soft mast) is a key food resource for many game and nongame wildlife species (Martin et al. 1951). Most species of birds and mammals consume fruit at least occasionally (Martin et al. 1951, Willson 1986). Fruit consumption has been linked to mammalian survival and reproductive success (e.g., Rogers 1976, Eiler et al. 1989). Fruit choice is a complex interplay between the nutritional composition of fruit, changing nutritional needs, availability of alternative food sources, and seasonal patterns of fruit and consumer abundance (Levey and Martinez del Rio 2001). Some studies suggest birds consume high-lipid fruits more rapidly than “low-quality” (low-lipid) fruits in fall (White and Stiles 1992), but others indicate nutritional quality is not an important determinant of fruit selection by birds (Borowicz 1988, Fuentes 1994, Jordano 2000, Whelan and Willson 1994). Further, digestive abilities may differ among avian species (Fuentes 1994, Martinez del Rio and Restrepo 1993). For example, Cedar Waxwings (*Bombycilla cedrorum*) specialize in sugary fruits, whereas thrushes specialize in lipid-rich fruits (Witmer and Van Soest 1998). American Robins (*Turdus migratorius*) produce low levels of the enzyme sucrase, and thus cannot digest high-sucrose fruits (Martinez del Rio and Restrepo 1993).

Abundant fruit in young forests may be a particularly important high-energy food source for neotropical migratory birds during fall migration (Parrish 1997). During winter, soft mast is important to many vertebrates when other food resources are scarce (e.g., McCarty et al. 2002, Greenberg and Forrest 2003, Whitehead 2003). For example, the local distribution of Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) during winter may be influenced by fruit availability (Kwit et al. 2004, Borgmann et al. 2004). The open conditions in young forests provide greater abundance of fruit, and also facilitate discovery by fruit-eating vertebrates. Fruit removal rates may be more rapid in gaps and along forest edges than under closed-canopy forests (Thompson and Willson 1978).

Fruit availability and abundance vary spatially and temporally across heterogeneous landscapes comprised of different forest age classes and site quality. This variation in fruit abundance results from differences in the composition of fruiting species, fruiting phenology, and the dynamic process of colonization and recovery of fruiting plants in young, recently disturbed forests. At local scales, fruit production is dictated by the composition of plant species, many of which are patchy in their occurrence.

Fruit production per hectare is inversely related to the residual density or basal area (BA) of overstory trees (shade) remaining after a disturbance, and declines over time with canopy closure (Perry et al. 1999, Fig. 8.1). Fruit production is much greater in forest openings than in closed canopy conditions, regardless of whether openings are caused by natural disturbance (e.g., Thompson and Willson 1978, Blake and Hoppes 1986) or by silvicultural disturbance, such as timber harvest (e.g., Lay 1966, Halls and Alcaniz 1968, Johnson and Landers 1978, Campo and Hurst 1980, Stransky and Roese 1984, Perry et al. 1999, Mitchell and Powell 2003, Greenberg et al. 2007). For example, Blake and Hoppes (1986) reported 44 fruits/80m^2 in single-tree gaps, but only 2 fruits/80m^2 in adjacent closed canopy forest in Illinois. Perry et al. (1999; *unpubl. data*) found that in the Interior Highlands of Arkansas and Oklahoma, production of dry edible fruit pulp biomass ($\leq$2 m height) 5 years post-harvest was about 3 times greater in group selection matrix (the forest surrounding group openings) and 8 times greater in single-tree selection harvests where BA reduction was minor and light increased only slightly, compared to mature (>50 years old), closed-canopy forest. However, dry edible fruit pulp biomass production ($\leq$ 2 m height) in their study area was 31 times greater in clearcuts, 46 times greater in group openings, and 49 times greater in shelterwood harvests than in mature forest (Figs. 8.2, 8.3). In the Southern Appalachians, production of dry edible fruit pulp biomass was 5 to 20 times greater in shelterwood harvests (with about 15% BA retention) beginning 3 to 5 years post-harvest than in mature forest (Fig. 8.3) (Greenberg et al. 2007). Increases in fruit production are generally less in small openings, such those created by single-tree selection or gaps compared to larger openings, such clearcut or shelterwood harvests, because smaller openings are typically shaded more by surrounding forest than larger openings (Perry et al. 1999).

Fruit production in young forests can be affected by the type of disturbance and prior land uses. In areas subjected to timber harvest, site preparation after harvest can affect the length of time plants take to establish fruiting or overall long-term fruit production. After logging, sites not subjected to site preparation or sites only burned after harvest may produce more fruit from woody shrubs than sites subjected to site preparation methods, such as mechanical chopping or blading, which destroy the roots of pre-established plants (Stransky and Halls 1980). However, more intense site preparation can potentially facilitate establishment of disturbance-adapted herbaceous plants from seed, such as pokeweed and blackberry. Seeds of these “pioneer” species are dispersed by vertebrates that eat the fruits, and can be abundant in seed banks prior to disturbances (T. Keyser, USDA Forest Service, *unpubl. data*). In reforested areas subjected to timber harvest, lands that were previously cleared and farmed produce substantially less fruit because of sparse seed beds and fewer pre-established root systems (Stransky and Halls 1980).

High-intensity (hot) fires in upland hardwood forests can create open, structurally diverse conditions by killing overstory and midstory trees. Burning in upland hardwood forests may reduce fruit production immediately following the fire, but may eventually result in increased production if light to the forest floor is increased and top-killed plants resprout, or disturbance-adapted species colonize or germinate from the seedbank, and fruit (Jackson et al. 2007, J Michael McCord, University of Tennessee, *unpubl. data*). More commonly, prescribed fires in upland hardwood forests are low-intensity with minimal disturbance or increases in light reaching the understory (Jackson et al. 2007). Post-burn increases in fruit production generally correspond with reductions in canopy cover and increased light to the forest floor, and thus are greater following high-intensity burns that kill trees. Post-burn fruit production may be spatially patchy (Jackson et al. 2007), reflecting the mosaic of light and disturbance conditions created by the patchy burn patterns typical in upland hardwood forests.

Burning at 7-year intervals or less in young forests may impede canopy closure and stimulate the development of herbaceous groundcover (Masters et al. 1993), thereby also prolonging young forest conditions that promote abundant fruit production. Prescribed fire may create opportunities for germination, establishment, and (or) growth for non-native invasive plant species, such as Russian and autumn olive (*Eleagnus* spp.) or oriental bittersweet (*Celastrus orbiculatus*), but it may also cause mortality or otherwise suppress population growth of many non-native species (D'Antonio 2000). A pre-fire inventory of non-native invasive plants and pre- or post-fire removal of highly invasive species may help to reduce the possibility of proliferation by some non-native species.

Total fruit production levels are typically tied more closely to stand age than to topographic position, and fruit production is generally highest in young forests (Reynolds-Hogland et al. 2006, Greenberg et al. 2007). In the Southern Appalachians, dry pulp biomass of fleshy fruit in young, recently harvested (using a low-leave shelterwood harvest where about 15% of the overstory BA was retained) stands is similar to that in mature forests during the first two years after harvest, but increases 5 to 20 fold by the third year after harvest (Greenberg et al. 2007; Fig. 8.3). Fruit production peaks around 5 to 8 years after harvest and remains high for several years before declining. By about the tenth year post-harvest, fruit production in young forests may be similar to production in mature, unthinned forests as growth of regenerating trees creates a fully shaded environment (Fig. 8.3). Reynolds-Hogland et al. (2006) found production of berries (*Gaylussacia* spp., *Vaccinium* spp., and *Rubus* spp.) was highest in 2–9 year old stands.

The length of time fruit production remains high in young forests varies with the growth rate of regenerating trees that eventually shade the forest understory. Woody plant growth rates are influenced by moisture or site quality, which is dictated by topographic position, soils, and geography (Elliott et al. Chapter 7, Loftis et al. Chapter 5). Thus, moist, high-quality sites may reach canopy closure and reduced fruit production more rapidly than xeric upland hardwood forests. Further, the occurrence and relative abundance of many fruit-producing species are influenced by site quality. For example, blackgum (*Nyssa sylvatica*) and ericaceous shrubs are most common on dry, lower quality sites in the Southern Appalachians, whereas spicebush and many herbaceous species are generally associated with moist, high-quality cove hardwood forests.

The disturbance-associated species pokeweed and blackberry are prodigious fruit producers in recently disturbed forests throughout the Central Hardwood Region, including the Southern Appalachians, Interior Highlands, Ridge and Valley, and upper Coastal Plain (Perry et al. 1999, Greenberg et al. 2007, Greenberg et al. *in review*, McCord and Harper *in press*). A "relay" between pokeweed and blackberry sustains high levels of fruit production in young hardwood forests for several years. Pokeweed dominates fruit production for the first few years after disturbance, but generally is shaded out by the fourth or fifth year. In contrast, blackberry is usually present, but takes three or four years before it produces substantial amounts of fruit. Sumac (*Rhus* spp.) is an ephemeral pioneer shrub that occurs throughout the Central Hardwood Region and produces prodigious amounts of fruit, but may occur less frequently in young forest patches than pokeweed and blackberry (Greenberg et al. 2007). In southern portions of the Central Hardwood Region, American beautyberry (*Callicarpa americana*) is also an important fruit producer in young forests.

Many species not typically associated with disturbance also produce abundant fruit in young forests -- often more fruit than in mature forests. In the Southern Appalachians, flowering dogwood (*Cornus florida*), American holly (*Ilex americana*), Fraser magnolia (*Magnolia fraseri*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and blackgum all produce fruit from stump sprouts within 1-3 years post-harvest. In the Interior Highlands, flowering dogwood, black cherry, sassafras, blackgum, serviceberry (*Amelanchier arborea)*, and muscadine grapes (*Vitis rotundifolia*) are species not associated with disturbance that can produce great amounts of soft mast in both older (7+ years old) openings and in mature forests (Segelquist and Green 1968, Rogers et al. 1990, Perry et al. 1999). Several herbaceous species that are generally associated with mature cove hardwood forests, including Jack-in-the-pulpit (*Arisaema triphyllum*), mandarin (*Disporum lanuginosum*), Solomon's seal (*Polygonatum commutatum*), and *Trillium* spp., also produce more fruit in recently-harvested forests than in mature forests (Greenberg et al. 2007).

Ericaceous shrubs, including huckleberry (*Gaylussacia* spp.) and blueberry (*Vaccinium* spp.), produce abundant fruit within a year after disturbance, but also produce a large proportion of the total fruit in mature forests. Dominant species include huckleberry in the Southern Appalachians, and deerberry (*V. stamineum*), which is widespread throughout the Central Hardwood Region. The relative abundance of huckleberry and blueberry species (and their fruit) varies with topography and geography. Huckleberry tends to be most abundant on dry, lower-quality sites. Blueberries produce minor amounts of fruit compared to huckleberry in the Southern Appalachians (Greenberg et al. 2007), though this may vary with location. They are the dominant ericaceous, fruit-producing species in the upper Coastal Plain and the Interior Highlands (Perry et al. 1999, Greenberg et al. *in review*).

Only a handful of native plant species in upland hardwood forests produce or retain fruit during winter. American holly, greenbriar (*Smilax* spp.), and sumac are important winter fruits throughout the Central Hardwood Region. Sumac is limited to recently disturbed forests, whereas holly and greenbriar produce fruit in all forest age-classes. Several species of non-native, invasive plants, including oriental bittersweet, Chinese privet (*Ligustrum sinense*), and multiflora rose (*Rosa multiflora*), produce or retain fruit during winter (Greenberg and Walter 2010) and can invade disturbed, or sometimes undisturbed, forests when these stands are near seed sources. Whereas these non-native plant species may provide food for wildlife, animals did not historically rely on those food sources and they are not part of the ecological balance that evolved between native animals and food sources in the Central Hardwood Region. Further, consumption of non-native fruits by birds and vertebrates promotes widespread dispersal and establishment of non-native plants across the landscape where they compromise native plant communities.

8.3 Hard Mast

Nuts produced by oak (*Quercus* spp.), hickory (*Carya* spp.) and beech (*Fagus grandifolia*) trees provide a valuable food resource to many wildlife species (Martin et al. 1951) and influence the distribution, recruitment and survival, and behavior of wildlife, ranging from migratory birds to black bear (*Ursus americanus*) (McShea and Healy 2002, Rodewald 2003, Clark 2004). Acorns are considered a "keystone" to biological diversity because their nourishment affects abundance of rodents that are an important prey base for raptors and carnivores, and affects populations of white-tailed deer (*Odocoileus virginianus*) that in turn alter forest structure and composition through browsing (Feldhamer 2002). Hard mast production may be reduced in young forests when mature oak, hickory, or other nut-producing trees are removed or killed. Thus, retention of some hard mast production when creating young forest stands through silviculture should be considered.

The age at which regenerating trees begin to produce mast varies; most oak species produce acorns by age 20-25 and reach full production potential around age 50 (Burns and Honkala 1990). Age of hard mast production, however, likely differs between trees that originate from seedlings versus stump sprouts (coppice) from rootstocks of mature, harvested trees. For example, coppice scarlet oaks and white oaks in the Appalachians produce abundant acorns within 25 years after harvest (Greenberg and Parresol 2002). Oak trees grown from seed in open conditions, such as nurseries, can produce acorns within 10 years (Scott Schlaurbaum, *unpubl. data*).

Some hard mast production can be sustained if mature, mast-producing trees are retained, such as in partial harvest techniques like shelterwood, single-tree selection, and group-selection harvests. The level of potential hard mast production depends partly on the number of mature mast-producing trees remaining after the disturbance, but is also affected by the selection of individual trees. Production of hard mast by retained trees in recently disturbed forests is confounded by various factors that affect nut production by individual trees, including tree size, genetics, and site quality. The influence of tree size (diameter at breast height; dbh) on acorn production is largely a function of crown area (Rose et al. *in review*). Larger-diameter oak trees generally have bigger crowns (Bechtold 2003) and thus can potentially produce more acorns than smaller-diameter trees. However, the influence of oak dbh on acorn density per unit of crown area is negligible (Greenberg and Parresol 2002, Lashley et al. 2010).

Generally <50% of individual oaks of any given species are "good" producers, yet the majority of the total acorn crop at a site may be produced by these trees (Greenberg and Parresol 2002, Lashley et al. 2010). Thus, high acorn production levels could be potentially sustained with the removal of ≥50% of individual oaks if good producers could be identified for retention (Lashley et al. 2010). Unfortunately, no measurable parameter can predict whether an individual oak is a good producer or a poor producer other than observation of individual trees over several years.

Any sustained post-harvest increase in acorn production by residual oaks or hickories is difficult to detect with confidence because of variation in hard mast production among individual trees and years. However, studies have established a clear relationship between forest density and seed production in pines (e.g., Croker 1952, Bilan 1960, Godman 1962), and foresters often thin pine stands to promote seed production.

Although few studies have evaluated the effects of stand density on mast production by oaks and hickories, some research suggests heavy thinning may increase hard mast production by individual trees (Paugh 1970, Healy 1997, Perry and Thill 2003). However, these reductions in tree density may reduce overall net production within a stand (Harlow and Eikum 1963, Minckler and McDermott 1960). Residual oaks and hickories may increase their production of nuts after thinning or timber harvests, likely a result of decreased competition, increased light to tree crowns, and possible increases in crown size over time (Perry and Thill 2003, Perry et al. 2004). Jackson et al. (2007) documented a 25% increase in crown size among white oaks retained following shelterwood harvest. Thus, reducing the BA of forests may increase production by the individual hard mast-producing trees that are left (Perry and Thill 2003; Fig. 8.4). Areas with reduced BA could potentially maintain similar hard mast production indices to areas of mature, unthinned forest because of the greater output by individual residual trees (Perry and Thill 2003), while at the same time promoting soft mast and forage production in the understory. Reduced hard mast production in individual harvested forest stands that comprise a small proportion of a forested landscape may be relatively inconsequential, and may be offset by a large increase in fleshy fruit production.

8.4 Herbaceous forage and woody browse

Many wildlife species, including white-tailed deer (*Odocoileus virginianus*), rabbits (*Sylvilagus* spp.), Ruffed Grouse (*Bonasa umbellus*), Bobwhite Quail (*Colinus virginianus*), black bear, Wild Turkey (*Meleagris gallopavo),* voles (*Microtus* spp.), and cotton rats (*Sigmodon* spp.), use various forbs, grasses, brambles, and browse (leaves and twigs of woody species ≤ about 1.4 m above the ground) to meet nutritional demands, and many other species require this low vegetative stratum for nesting, food (soft mast, seeds, and arthropods), and cover from predators.

Several studies within the Central Hardwood Region have evaluated forage availability following thinning and timber harvests (Morriss 1954, Ripley and Campbell 1960, Patton and McGinnes 1964, Della-Bianca and Johnson 1965, Moore and Downing 1965, Moore and Johnson 1967, Harlow and Downing 1969, 1970, Beck and Harlow 1981, Ford et al. 1993, Tilghman 1989, Johnson et al. 1995, Lashley et al, in press). Substantial reductions in BA significantly increase light to the forest floor and stimulate growth and development of the understory (Morriss 1954, Ford et al. 1993, Loftis et al.

Chapter 5, Elliott et al. Chapter 7). In Texas pine-hardwood forest, forage production (herbaceous and woody vegetation <1.5 m height) increased eightfold to twelvefold - from 309 to 383 dry kg/ha (preharvest) to 1983 to 3774 dry kg/ha - within 1 to 4 years after clearcutting and site preparation (Stransky and Halls 1978). In the Tennessee Ridge and Valley, forage availability (2008), dominated by tree species, was 5 times greater in shelterwood harvests (2001) followed by prescribed fire (2005) compared to mature forest controls (722 dry kg/ha versus 129 kg/ha, respectively), and more than 7 times greater in retention cuts followed by multiple burns (2001, 2005, 2007) compared to controls (940 dry kg/ha versus 129 kg/ha, respectively) (Lashley 2009). In the pine-hardwood forest of the Ouachita Mountains in Oklahoma, total mean forage availability was 16 to 24 times greater in stands where pine timber was harvested, hardwoods thinned, and winter prescribed burns conducted at 1, 2, 3, or 4-year intervals (2 to 4 times) compared to mature forest controls (2,832 to 4,123 dry kg/ha versus 171 kg/ha, respectively); grasses composed the majority, whereas woody vegetation composed a small fraction of total forage (Masters et al. 1993). Forage availability in young forests declines appreciably after canopy closure (within 7 to 10 years), when sunlight no longer reaches the forest floor, but gradually increases, albeit to a relatively lower level, as stands mature (Johnson et al. 1995, Beck 1983).

Site quality can have a significant effect on forage availability (Beck 1983). Herbaceous plant diversity and quantity may be greater on mesic, high-quality sites than on dry, low-quality sites (Elliott et al. Chapter 7). In contrast, woody sprouts generally dominate on dry, poor-quality sites after heavy thinning (Beck 1983, Crawford 1976). Post-disturbance production of grasses and forbs may vary geographically, and with disturbance types and frequency (such as fire) (Spetich et al. Chapter 4).

In the Southern Appalachians nutritional quality of leaves from 5 woody browse species was similar between recent clearcuts and mature forest (Ford et al. 1994). However, forage quality may be greater in young forest than in mature forest because of increased diversity of forbs and other shade intolerant plant species (Elliott et al. Chapter 7). In addition, a high density of stump sprouts or seedlings in young forest increases browse availability from species such as blackgum, red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), oak, and hickory (Harlow and Hooper 1972, Warren and Hurst 1981, Beck and Harlow 1981, Ford et al. 1994, Loftis et al. Chapter 5). Forage quality for a given species, whether herbaceous or woody, is related to stage of growth. New growth of any plant is more digestible than older growth; as plants mature, cell walls thicken and lignin content, which is relatively indigestible, increases (Ball et al. 2002). Thus, greater forage quality and nutritional carrying capacity of young forests compared to mature forests is related to increased plant diversity, young foliar growth, and higher biomass resulting from increased available sunlight.

Without periodic disturbances, woody vegetation grows into the midstory (Jackson et al. 2007), reducing forage availability and a thick understory structure that benefits several forest songbirds and other wildlife species (Della-Bianca and Johnson 1965, Jackson et al. 2007, Thatcher and Buehler 2007, Lashley 2009, Shifley and Thompson Chapter 6, Franzreb et al. Chapter 9). Intense fire that kills trees, or timber stand improvement treatments, such as heavy thinning or retention cuts, can create or perpetuate open-canopy conditions typical of young forests. Low-intensity prescribed fire in hardwood stands with an incomplete canopy cover can also maintain a diverse understory structure for various wildlife species without harming the residual overstory (Jackson et al. 2007). Repeated low-intensity prescribed fire within a 7-year period following canopy reduction will also sustain greater forage production by impeding canopy closure (Lashley et al. *in press*). Without a reduction in canopy closure and an increase in available sunlight, low-intensity prescribed fire is relatively ineffective in maintaining high forage production and diverse understory structure (Jackson et al. 2007, Shaw et al. 2010, Lashley et al. *in press*).

8.5 Arthropods

Arthropods are an important food source for many vertebrates. Most bird species in temperate deciduous forests are primarily insectivorous during the breeding season, and reproductive output may be limited by low food abundance (Holmes et al. 1986). Small, litter-dwelling arthropods are important for terrestrial salamanders (Duellman and Trueb 1986), whereas larger ground-dwelling arthropods are consumed by many birds, mammals, and larger amphibians and reptiles (Martin et al. 1951). Flying and foliar arthropods, such as Lepidoptera and Diptera, are important for many species of insectivorous birds and bats (Rodenhouse and Holmes 1992, Kurta et al. 1990, Loeb and O'Keefe Chapter 10). Soil arthropods, such as larval beetles, are important components of skunk (*Mephitis* spp.) and shrew (Soricidae) diets (Martin et al. 1951). Forest condition and microclimate requirements differ among orders, families, and even species of arthropods (Greenberg and Forrest 2003). Therefore, forest disturbances that create open-canopy conditions have different effects on arthropod guilds, or groups, according to their habitat requirements. Disturbances that increase protective cover may benefit vertebrates that forage for arthropods and thus functionally increase invertebrate availability (Jackson et al. 2007).

Results of studies on arthropod response to forest disturbances have been inconsistent. Discrepancies may result from differences in sampling methodologies, site quality, season or month(s) studied, and timing of disturbance. For example, litter extraction methods sample the abundance of litter-dwelling arthropods as a snapshot in time, whereas pitfalls and other trapping methods sample a combination of both arthropod abundance and activity levels (Swengel 2001). Efficiency of sweep net sampling, area sampled, and forest strata sampled may differ among vegetation types because of differences in vegetation structure, thus biasing results (Harper and Guynn 1998). Insect activity periods differ among orders and species and studies conducted during different months may not be directly comparable. Disturbances that occur during peak activity periods or affect arthropod food sources could have a greater impact than disturbances during the non-growing season. Despite these types of inconsistencies, some general themes emerge, with overall responses to high-intensity disturbances and young forest conditions differing among litter-dwelling, ground-dwelling, and flying/foliar arthropods.

Forest disturbances that reduce canopy cover, increase light, and increase temperature at the forest floor, may result in decreased depth, cover, and moisture of leaf litter and cause declines in the biomass of litter- and ground-dwelling arthropods. Post-harvest reductions in leaf litter depth reported in the literature range from 14–70%

(Buckner and Shure 1985, Ashe 1995), and may vary with site quality and the size and type of disturbance. However, the rapid growth of stump sprouts and other vegetation (Loftis et al. Chapter 5, Elliott et al. Chapter 7), and residual mature trees provide shade and replenish the leaf litter through leaf fall within 1-2 years post-disturbance (e.g., Greenberg and Waldrop 2008, Greenberg et al. 2010).

Ground- and litter-dwelling arthropod abundance and biomass is positively associated with leaf litter depth and moisture. For example, when compared to mature forests, arthropod abundance or biomass is lower in large forest gaps created by wind disturbance (Greenberg and Forrest 2003), on unpaved roads and up to 100 m into the adjacent mature forest (Haskell 2000), in managed and unmanaged forest openings (Harper et al. 2001), and recently harvested cove- and upland hardwood forest stands (Whitehead 2003). Several orders, such as Carabidae, Julida, Scolopendromorpha, and Spirobolidae, may be more abundant in mature forests where leaf litter depth and cover are greater (e.g., Greenberg and Forrest 2003), but other orders, such as Orthoptera and Homoptera may be more abundant in disturbed forests with greater cover of forbs and young foliage (e.g., Hollifield and Dimmick 1995).

Burning may have short-term negative impacts on litter- and ground-dwelling macroarthropod communities by direct mortality, or indirectly by altering forest floor conditions. Impacts of burning also correspond with the intensity and patchiness of burns, the availability of refugia, such as coarse woody debris, and the timing of burns in relation to taxon-specific life history traits (Swengel 2001). For example, burning during winter may affect ground-dwelling macroarthropods less because most of these species (including eggs and larvae) are underground and activity levels are generally low (Greenberg and Forrest 2003). Thus, life history traits, mobility, and behavior can mitigate direct effects of burning on arthropods.

Early spring burns may have little detectable impact on the relative abundance of ground dwelling arthropods (Coleman and Rieske 2006, Greenberg et al. 2010). However, Kalisz and Powell (2000) reported a 36% reduction in total dry biomass of forest floor and soil invertebrates after a March burn on the Cumberland Plateau in Kentucky, primarily from reductions in Coleopterans and Coleopteran larvae. Litter-dwelling arthropods, such as springtails, may be more sensitive to prescribed fire than ground-dwelling arthropods. For example, single and multiple prescribed burns in early spring reduced litter-dwelling arthropod abundance by 83% the first year and 48% the second year after burning in upland forests on the Cumberland Plateau in southeastern Kentucky (Coleman and Rieske 2006). Dress and Boerner (2004) reported lower relative abundance of microarthropods in an annually burned watershed where leaf litter mass was reduced, compared to periodically burned and unburned watersheds in southern Ohio. However, reduced leaf litter cover may increase arthropod availability to predators (Harper et al. 2001). Nevertheless, post-burn recovery of leaf litter arthropods is rapid and corresponds with leaf litter replenishment the following year (K. Reynolds, University of North Carolina at Asheville *pers. comm.*).

Abundance and species richness of flying/foliar arthropods is often associated with plant species richness and herbaceous groundcover because many of these arthropods feed on foliage of specific plants, pollen, or nectar of woody and herbaceous plants. For example, abundance or species richness of foliage- or floral-feeding arthropods tends to be lower in pasture monocultures (Hollifield and Dimmick 1995, Burford et al. 1999, Harper et al. 2001, Fettinger et al. 2002, Dodd et al. 2008). In the Central Hardwood Region, disturbance does not usually change species richness of woody plants (Loftis et al. Chapter 5), but may increase richness of herbaceous plant species (Elliott et al. Chapter 7) or stimulate flowering and fruiting. In the southern Appalachains, the abundance of floral-visiting insects increased following hot prescribed fires that killed trees and increased herbaceous cover (Campbell et al. 2007). In the Ozark Mountains, moth occurrence was correlated with density and richness of woody plants, though abundance was similar among forest age classes (Dodd et al. 2008). Species richness and diversity of butterflies and their food- and host plants was higher in South Carolina early successional utility rights-of-way (Lanham et al. Chapter 12). In contrast, the abundance or species richness of foliage- or floral-feeding arthropods tends to be lower where forest stands are converted to pasture dominated by graminoids of homogeneous composition (Hollifield and Dimmick 1995, Burford et al. 1999, Harper et al. 2001, Fettinger et al. 2002, Dodd et al. 2008).

Site quality may influence arthropod availability because of potential differences in herbaceous cover and richness, leaf litter depth, and moisture that are associated with topographic position (Harper et al. 2001). In one study, three times more invertebrates occurred in mesic than xeric forest types, which in turn corresponded with herbaceous cover (Healy 1985). Other studies indicate that stand age is most important in determining arthropod abundance. In the Southern Appalachians, mature upland- and cove hardwood forests had more litter-dwelling arthropods and fewer flying/foliar arthropods than young upland- or cove hardwood forests (Whitehead 2003).

8.6 Small mammals

Terrestrial small mammals (rats, mice, voles, shrews, squirrels, and rabbits) are the primary prey base for many species of vertebrates, including snakes, hawks, owls, and mammalian carnivores. For example, small mammals comprised 63% of Red-tailed Hawk (*Buteo jamaicensis*) diets in hardwood forests of Pennsylvania (Sutton 1928), 76% of copperhead (*Agkistrodon contortrix*) diets in hardwood forests of Tennessee (Garton and Dimmick 1969), and occurred in 13% of coyote (*Canis latrans*) stomachs (Gipson 1974) and 65% of bobcat (*Lynx rufus*) stomachs (Fritz and Sealander 1978) examined in Arkansas. Consequently, small mammals may be considered a food source, and their abundance may be viewed as food biomass for many predators.

Species of small mammals respond differently to young, open-canopy conditions created by forest disturbance throughout the Central Hardwood Region. In deciduous forests, some groups of small mammals (e.g., *Peromyscus*) may decline after intense disturbances (Kirkland 1990); however, overall abundance of small mammals as a group (with the exceptions of squirrels [*Sciurus* and *Tamiasciurus*]) is generally much greater in young, recently disturbed, open-canopy forests compared to mature, closed-canopy forests. For example, Kirkland (1990) evaluated 21 studies on effects of clearcutting on small mammals (rodents and sorcids) in North America and found a significant pattern of increased relative abundance of all species combined after clearcutting. Furthermore, he found three out of four studies examining small mammal density reported increases after clearcutting. In hardwood forests of West Virginia, captures rates of all small mammals combined were 50% greater in 8–9 year-old stands than in mature (>100 years old) stands

(Healy and Brooks 1988). In the Interior Highlands of Arkansas and Oklahoma, overall abundance of small mammals is low in mature, closed-canopy forests (Perry and Thill 2005); however, reductions in BA via timber harvest can dramatically increase overall abundance. Capture rates of all small mammals combined in areas harvested via single-tree selection, group selection, shelterwood cuts, and clearcuts can be 4 to 7 times greater than in closed-canopy, mature forest (Perry and Thill 2005). Young forests provide the necessary habitat features for many species of small mammals. Abundance of some small mammals is correlated with coarse woody debris and logs (e.g., Loeb 1999, McCay 2000), and abundant woody debris often results from natural disturbances, such as windstorms or fires, or by logging and its associated slash. Shrub cover is also an important habitat component for many small mammals (e.g., Healy and Brooks 1988, Carey and Johnson 1995, Bellows et al. 2001), and shrub cover is characteristically much greater in young forests than mature, closed-canopy forests. Increased food supply typically results in increased vertebrate density (Boutin 1990), and abundant hard mast, soft mast, and grass/weed seeds in young, recently disturbed forest may provide substantially more food for small mammals than in surrounding mature forests. Furthermore, many small mammals, including voles, rabbits, and cotton rats, are primarily herbivores, and young, recently disturbed, open-canopy forest may provide substantially more herbaceous vegetation than mature forests. Declines in rabbit numbers in the eastern United States are attributable to changing land practices that reduced habitat, such as young forests, which provide critical cover for winter survival and predator evasion (Litvaitis 2001). Consequently, young hardwood forests provide abundant structural components and the necessary foods to support relative large densities of small mammals.

Many species of small mammals are associated with grasslands or hayfields (e.g., Hamilton and Whitaker 1979, Sealander and Heidt 1990), and in their earliest stages of development, young forests may provide habitat similar to grasslands (abundant herbaceous vegetation) and attract species such as hispid cotton rats (*S. hispidus*) and deer mice (*Peromyscus maniculatus*). A portion of the increase in small mammal abundance in young, recently disturbed forest may be attributable to exploitation of these sites by non-forest small mammals, such as jumping mice (*Zapus* spp.) and voles (Kirkland 1990).

Predator activity may be greatest in areas with the most prey (e.g., Ozoga and Harger 1966, Litvaitis and Shaw 1980), and predators of small mammals are often abundant in early successional habitat where they take advantage of abundant prey and cover. Many predators of small mammals, including gray fox (*Urocyon cinereoargenteus*), bobcats, and many snakes use young forests, shrubby areas, or areas with dense understories for cover (e.g., Hamilton 1982, Haroldson and Fritzell 1984, Kjoss and Litvaitis 2001, Perry et al. 2009) or avoid open areas with little cover (e.g.,Weatherhead and Prior 1992). For example, bobcats often prefer brushy areas or regenerating clearcuts where prey is most abundant (e.g., Hamilton 1982, Rolley and Warde 1985, Chamberlain et al. 2003). Furthermore, abundant burrows created by small mammals in areas of high small mammal abundance may provide habitat for predators such as snakes (Perry et al. 2009). Thus, young forest and other early successional or shrubby areas provide habitat for many predators of small mammals.

8.7 Conclusion

Young upland hardwood forests of the Central Hardwood Region provide a number of functions important to many wildlife species. These young forests provide habitat necessary for many species, including dense cover, abundant shrubs for shrub-nesting birds, and open areas for aerial predators, and also function as high-quality food patches that generally provide greater levels of many food resources than mature forests. Food resources abundant in young upland hardwood forests include fleshy fruit, forbs and grasses , browse, arthropods, and small mammals. Continuous creation of young forest patches through natural and silvicultural disturbance creates a shifting mosaic of age-classes and patch-sizes across the forested landscape. Partial reductions in tree density or canopy cover created by windstorms, hot fires, or partial timber harvests can provide a complex, heterogeneous forested landscape. Reductions in overstory tree density, while retaining some hard mast-producing trees, can promote production of fleshy fruit, foliage and flowers, and increase densities of arthropods and small mammals, while maintaining some level of hard mast production. Over time, young stands mature and provide other important features, such as high stem densities for grouse (Jones et al. 2008), or mature forest conditions that provide habitat for "forest interior" bird species (Greenberg and Lanham 2001). Balancing the creation of young, recently disturbed forest areas with the desired amount and distribution of other forest age classes will sustain high-quality food patches for wildlife within a landscape context.

8.8 Literature Cited

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Fig. 8.1 Relationship between total fruit production (dry edible pulp biomass; kg/ha <2 m high) and overstory BA (m^2/ha) in forest stands thinned/harvested to various densities in the Interior Highlands of Arkansas and Oklahoma. Production was greatest in stands with lowest BA, but the relationship changed over time since disturbance with the strongest relationship at 5 and 8 years after disturbance (data from Perry et al. 1999 and Perry unpublished data).

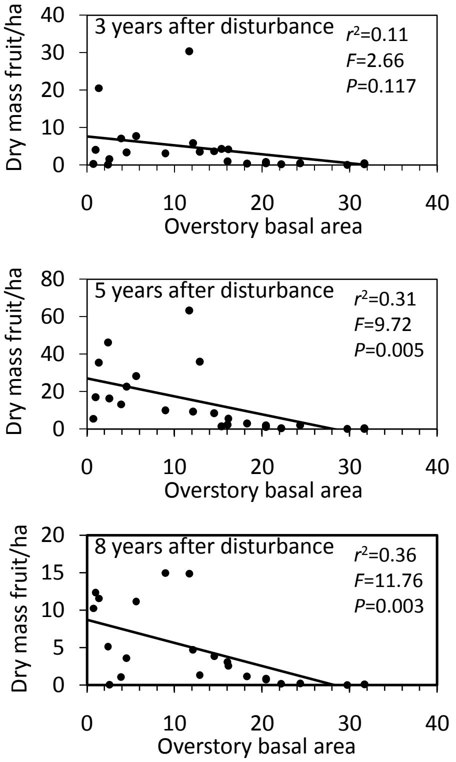

Fig. 8.2 Mean total dry biomass (kg/ha) of edible pulp from fleshy fruit (≤2 m high) produced 1, 3, 5, and 8 years after harvest in different silvicultural treatments with different average retained BAs in the Interior Highlands of Arkansas and Oklahoma. Treatments are unharvested forests (control; 29.4m^2/ha BA), the forested matrix surrounding group openings in group-selection stands (group matrix; 20.3m^2/ha BA), single-tree selection stands (15.5m^2/ha BA), group openings (4.1 m^2/ha BA), shelterwood stands (11.4 m^2/ha BA), and clearcuts (1.4m^2/ha BA). Data from Perry et al. 1999 and Perry unpublished data.

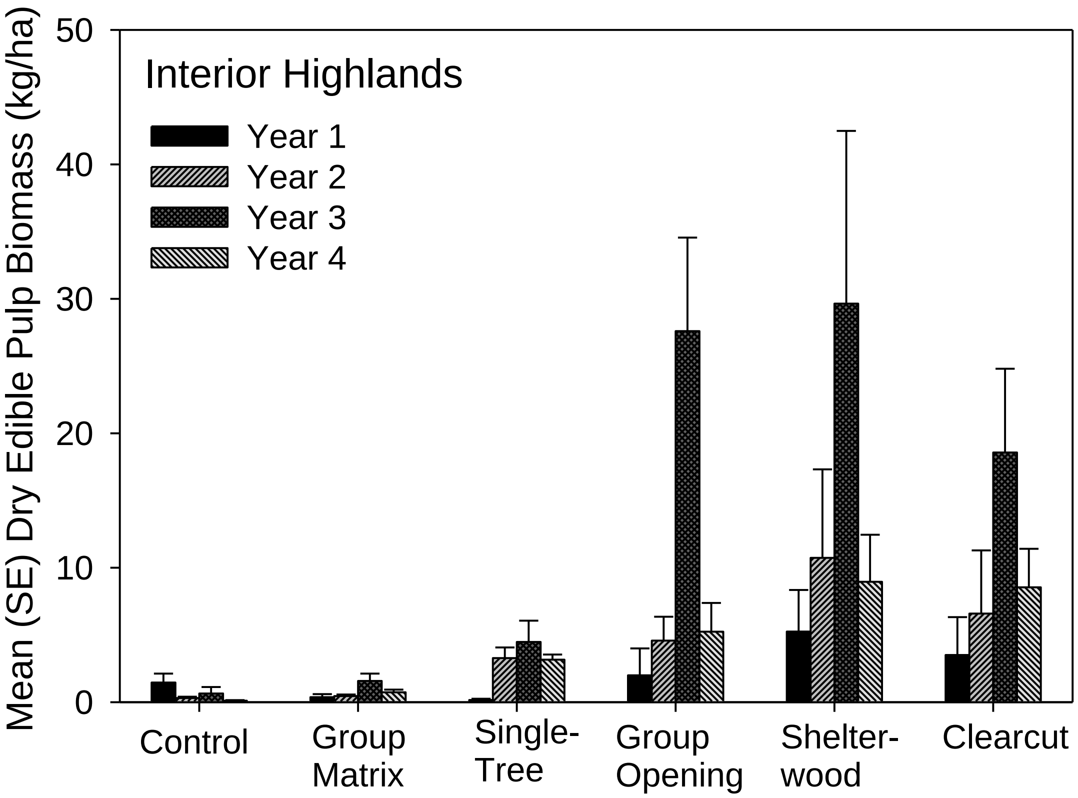

Fig. 8.3 Mean total fruit production (dry edible pulp biomass; kg/ha) produced 1, 2, 3, 4, 5, and 10 years after two-age harvests and in mature forest in upland hardwood and cove hardwood forests of the Southern Appalachians (data from Greenberg et al. 2007)

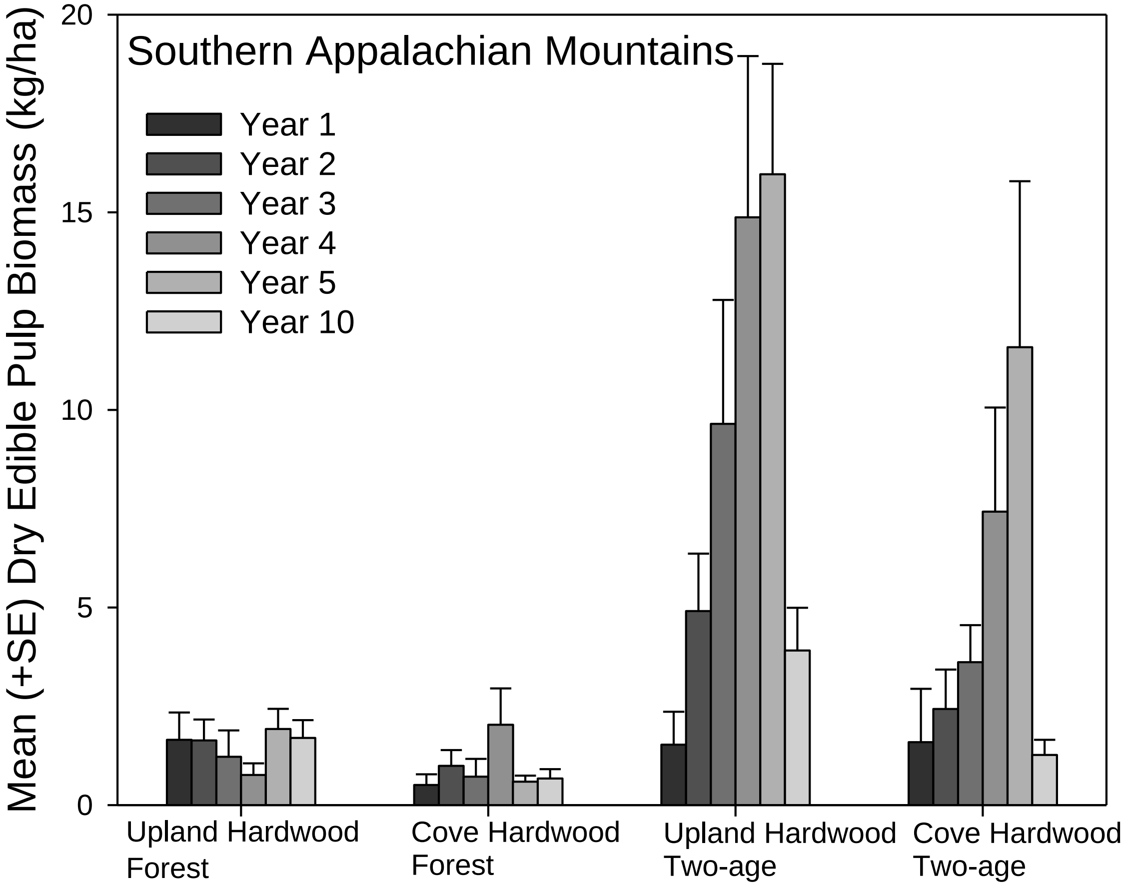

Fig. 8.4 Relationship between BA and indices of mean hard mast production per tree for white oaks (*Quercus alba*) in 13–15 forest stands differing in total BA in the Interior Highlands 1, 2, 3, 4, and 5 years after partial harvest and thinning (data from Perry et al. 2004). Annual differences in overall mast production among all areas demonstrate annual variation in mast production regardless of BA, which can be great.