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Forest Island Edges—Their Structure, Development, and Importance to Regional Forest Ecosystem Dynamics

J. Warren Ranney

Environmental Sciences Division
Publication No. 1069

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FOREST ISLAND EDGES - THEIR STRUCTURE, DEVELOPMENT, AND IMPORTANCE TO REGIONAL FOREST ECOSYSTEM DYNAMICS[1]

J. Warren Ranney[2]

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FOREWORD

This is a review of selected references pertaining to forest edge. Identification of the dynamics and functional role of forest edges is relatively new and has thus been synthesized from diverse literature sources, some of which have only small sections pertinent to the subject matter. Forest edges have been studied at many levels of detail which are presented here in a fashion that leads to the possible effects of edge on regional forest dynamics.

This literature review was prepared in initiating research at Oak Ridge National Laboratory and in continuing work leading to a Ph.D. in ecology at the University of Tennessee.

ABSTRACT

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Forested tracts surrounded by non-forested land develop characteristic edge habitats. These habitats often differ from interior forests in: (1) tree species composition, (2) primary productivity, (3) structure, (4) development, (5) animal activity, and (6) propagule dispersal capabilities. The differences vary according to edge aspect, the way a forest boundary may be structurally maintained by man, and the composition and age of a forest when an edge is created. Edge habitats may vary from 5 to 20 meters wide and, in the case of small forest islands of about two hectares or less, the entire island may display edge conditions. Side-lighting increases the amount of light an edge receives to the point of increasing primary productivity above normal interior forest rates even though dessication may lessen maximal productivity. These edge conditions have been characterized in the literature by the presence of shade-intolerant, xeric-tolerant tree species normally associated with early stages of forest development. The majority of the forest islands examined have been at near-climax states of development, while the edges of these islands did not exceed a maximum age of 100 years. It is not known if forest edge development reaches an equilibrium similar to states attained by adjoining forest interiors.

In some landscapes dwindling interior forest habitats are becoming more widely spaced, while the proportional area of edge is increasing. Edges receive stronger winds than interiors and are often more frequently visited by potential seed-dispersing animals. This suggests that the inter-island seed rain is strongly comprised of seeds from edge plants. Cautious applications of island biogeography theory indicate that regional forest development may be altered in favor of "edge" species because of the presence of extensive edge habitats and

their effect on propagule dispersal between forest islands. The contributions and effects of edge habitats on propagule dispersal and subsequent regional forest development have not been considered in the literature.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Since the European settlement of North America, many forested regions have been cleared for agriculture, resulting in a new and greatly changed environment (Baker and Dill 1970, 1971a, b). In many of these regions, extensive forests have been reduced to widely dispersed woodlots, fencerows and urban forests (Pollard 1973). For example, Curtis (1956) described a township in Green County, Wisconsin in which 70% of the forest had been cleared by 1882, 90% cleared by 1902, 95% cleared by 1935, and 96% had been cleared by 1950. The remaining tracts maintain the seed stock on which native forests depend for continued existence and for colonization of abandoned or naturally developing sites. Such alteration of the density and distribution of the native tree species within a region probably alters forest development considerably.

Edges of isolated forest stands, bounded by open, non-forest lands, reflect steep gradients of temperature, wind flow, moisture, and solar radiation occurring between the extremes of open land and forest interiors (Wales 1972). Smaller stands may be subjected to little climatic amelioration throughout. Ecotones develop as the vegetation responds to the microclimatic gradients. Structural and compositional changes occur as the vegetation at the forest boundary matures and takes on characteristics peculiar to edges (Gysel 1951, Trimble 1966). These ecotones buffer forest interiors from the conditions of the non-forested landscape (Levenson 1976, Bruner 1977).

By insulating the forest interior from wind, these ecotones (or edges) may often effectively reduce the wind dispersal of propagules from interior trees. Simultaneously, the dispersal of propagules from edge trees may be enhanced by their high exposure to wind dispersal vectors. In addition, visitations by wide ranging animals may be more intense at forest edges than in the forest interior. Animal transport of propagules is known to play an effective part in the dispersal of certain propagules (Auclair and Cottam 1971, Howe and Primack 1975). These aspects of forest edges are particularly important in landscapes where propagules must travel rather large distances to reach other forest stands and thus have a chance of establishment. I hypothesize that forest edges provide a greater number of propagules per unit area to inter-stand seed exchange compared to forest interiors. Edges that are 75-100 years old are known to generally have a different species composition than interior forests (Wales 1972). In landscapes of widely scattered forest islands having edges of this age, the dispersal and invasion of propagules between islands would be dominated by propagules of edge species. Potentially, a compositional change in regional forests through time and space could result from changed species invasion rates (MacArthur and Wilson 1967), compared to presettlement forest conditions.

What are the characteristics and functions of edges in regions where forests occur in spatial arrangements unlike those in which they evolved (Darlington 1965)? Gysel (1951) and Leopold (1933) were the first to seriously begin work identifying the structure, composition, and role of forest edges occurring next to maintained fields. Recent studies applying the concepts of island biogeography to terrestrial ecosystems (Vuilleumier 1970, Brown 1971, Diamond 1976) have stimulated investigation of forested islands embedded in an agricultural landscape (Forman and Elfstrom 1975, Galli, Leck and Forman 1976, Tramer and Suhrweir 1975, Suhrweir and Tramer 1976). These studies have renewed interest in the characteristics and importance of forest edges (Wales 1972, Levenson 1976, Ghiselin 1976, Bruner 1977).

CONCEPTS OF FOREST EDGE

Forest edges have been variously described depending on scale and vegetation physiognomy. They have been considered the transition zones between major plant communities such as the prairie-forest border in Minnesota and in Wisconsin (Whitford 1949, Curtis and McIntosh 1951, Buell and Cantlon 1951, Curtis 1959). Barick (1950) described forest edge as an ecotone between two vegetation types, both of which could be forests. The vegetational and microclimatic gradient along the periphery of (and within) a forest adjacent to a non-forested system (e.g., powerline and road rights-of-way, agricultural fields, and other maintained clearings) (Wales 1972, Bruner 1977) is the type of edge considered in this paper. Therefore, in this concept, the edge community is bounded on one side by non-forested land and on the other side by a forest interior. The interior forest has been considered relatively unaffected by the adjacent open land system (Bruner 1977), provided that the forest is of sufficient size (Levenson 1976). Although not often stated, this concept of forest edge has been the one most widely accepted and is supported by results from studies by Gysel (1951), Geiger (1966), and Wales (1972).

Probably the best known concept of "edge effect" was initiated by Leopold (1933). Identified as the "law of interspersion," this concept suggested that high species diversity was the result of overlap of different habitats (Allen 1962, MacArthur and Pianka 1966). It was soon realized that quantifying perimeters was a way of identifying the extent of the "edge effect" or species diversity (Kelker 1964). Patton (1975) described a method of quantifying habitat edge through a diversity index based on the ratio of the perimeters of two equal sized areas, one a circle and the other the plot being examined. The circle was used to represent the minimum perimeter of a two-dimensional area. Ghiselin (1977) recently suggested that an edge index based on the amount of edge or ecotone present could be used as an indicator of relative animal productivity between similar habitats. The approach is based on the historically supported point that ecotones are generally more productive because they contain more species, receive more solar energy, and represent and inter-grading of two habitats.

The structure of edge and its high productivity (Levenson 1976) have caused some (Karr 1971, Karr and Roth 1971) to attribute high animal species diversity to these vegetational factors and the "law of interspersion." McDiarmid, et al. (1977) found that fruit crop size was greatest in pasture-edge trees and smallest in forest trees for a species having bird-dispersed fruit. He and others have also found that peak propagule production attracts animal predation. This may be one cause of the edge effect. Diverse opinions exist on the definition of edge as a habitat and its values to wildlife. It has been considered a "distinct" habitat in itself (Johnston 1947) which, in combination with its proximity to diverse habitats, served as a more usable habitat for many animals (Odum 1959, States 1976). Wales (1972) considers edge to be an ecotone between forests and open fields in which tree species representative of open, pioneer forest development occur with shade tolerant mesic forest species common to forest interiors. For wildlife, edge is often treated as the overlap of two habitat types in which wildlife species associated with each habitat also overlap (Odum 1959, Schreiber et al. 1976, Johnson et al. 1977).

The applications of the concepts of edge to other aspects of modern ecology have been largely ignored. The failure to combine or synthesize independently collected information on plant and animal interactions has been the principle block to a more profound consideration. However, new concepts in niche quantification and studies of the effects of animals on tree seed dispersal and mortality (Howe 1977, Reichman and Oberstein 1977, Mitchell 1977, Bullock and Primack 1977, Wall and Balda 1977) are bringing concepts of forest edge and forest development closer to a holistic (or systems) definition rather than a strictly faunal or botanical definition.

ENVIRONMENTAL FORCES SHAPING EDGE

Wind

Work on the relationships between shelterbelts and wind movement (Van Haverbeke 1973, Uskov et. al. 1974) indicates that edge trees modify wind flow around, through, and over stands in addition to absorbing much of the lateral wind force (Bergen 1976). Kittredge (1948) showed that wind speed was scarcely affected just above the top of a single semi-permeable barrier; however, wind speed slowed above and behind a barrier for a considerable distance (Figure 1). In a laboratory experiment, Moen (1974) showed that the upper part of wind barriers simulating forest stand edges receive a large portion of

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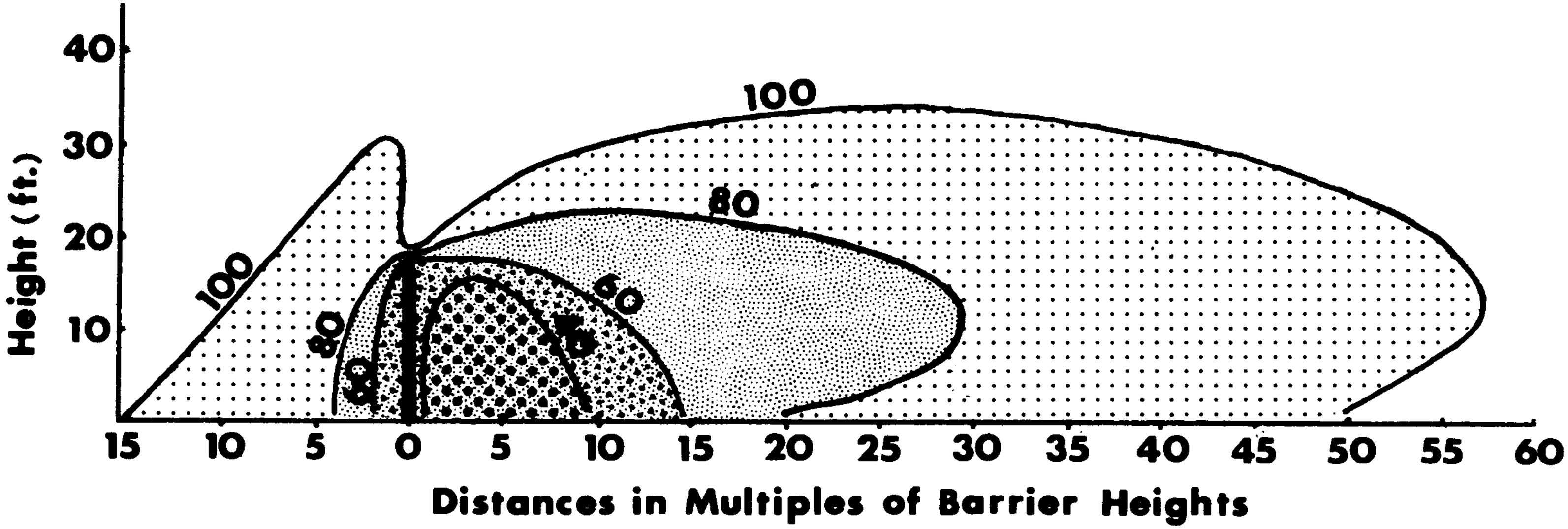

Fig. 1. The distribution of wind velocities around a half-solid barrier are expressed as percentages of velocities in the open at corresponding heights. The vertical scale is eight times the horizontal (after Kittredge 1948).

lateral wind force. He demonstrated the importance of the permeability of wind barriers to air movement on the leeward side of these barriers (Figures 2 and 3). The more permeable a barrier is to horizontal wind flow (up to 47 percent permeable or open), the more reduced is the air circulation on the immediate leeward side of the stand. As velocity increases, the circulation pattern extends a greater distance downwind from the barrier (Figure 2) (Moen 1974). Kawatani and Sadeh (1971) found that canopy roughness and diversity were inversely related to wind flow within the canopy while Bergen (1976) found canopy roughness to increase turbulence over a stand.

Greater wind velocity occurs at forest edges than in forest interiors (see Hutchison and Matt 1976b for forest interior velocities) creating more xeric conditions in and near edges (Curtis 1959, Geiger 1965, Lowry 1970). Kittredge (1948) described wind velocities inside the edge of a stand as being anywhere from about 15 to 3 percent of outside wind speed. The drought conditions affecting edge trees may result from increased evapotranspiration which places a demand on edge soil moisture. For one tree species, Liriodendron tulipifera, McConathy et al. (1976) showed that calculated diffusion resistance values across leaf stomatal openings decreased as wind speeds increased to about 100 cm. per second. Similarly, calculated boundary layer resistance values also decreased but continued decreasing in wind speeds up to 500 cm/sec. Edge exposure to wind thus acts to increase edge evapotranspiration over interior rates. The extent of the drying effect is dependent on the density of vegetation, the prevailing wind direction and velocity, and forest island size and shape. Small forest stands may be permeable enough to wind that xeric conditions extend throughout the stand, and may be expressed through changes in tree composition (Auclair and Cottam 1971, Schmid 1975, and Levenson 1976).

The effect of wind on forest stand edge temperatures during the growing season is dependent on wind velocity and temperature differences between the stand edge and exterior (Geiger 1965). Diurnal variations in solar radiation and air circulation at edges are wider than in forest interiors. Consequently, edges are areas of greater environmental stress. Crockett (1971) has described the effects of

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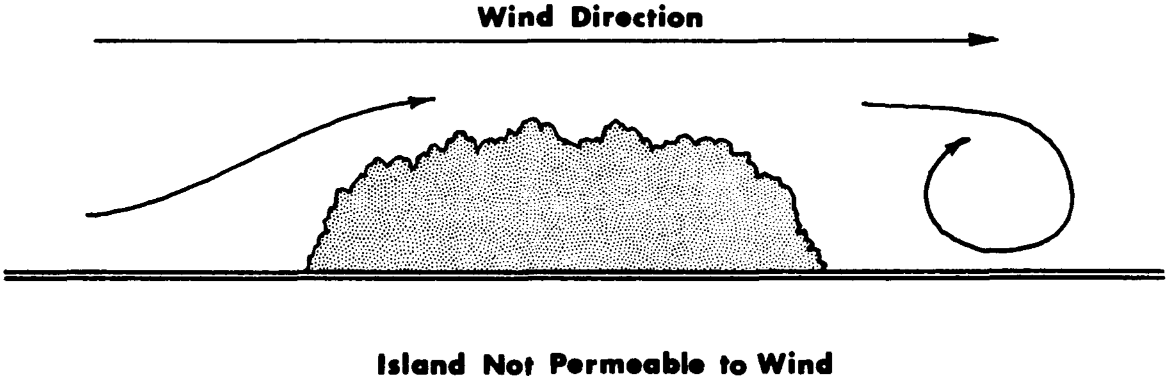

Fig. 2. Air movement over forest islands changes with windspeed. During higher winds the circular air movement on the leeward side of the island moves further downwind.

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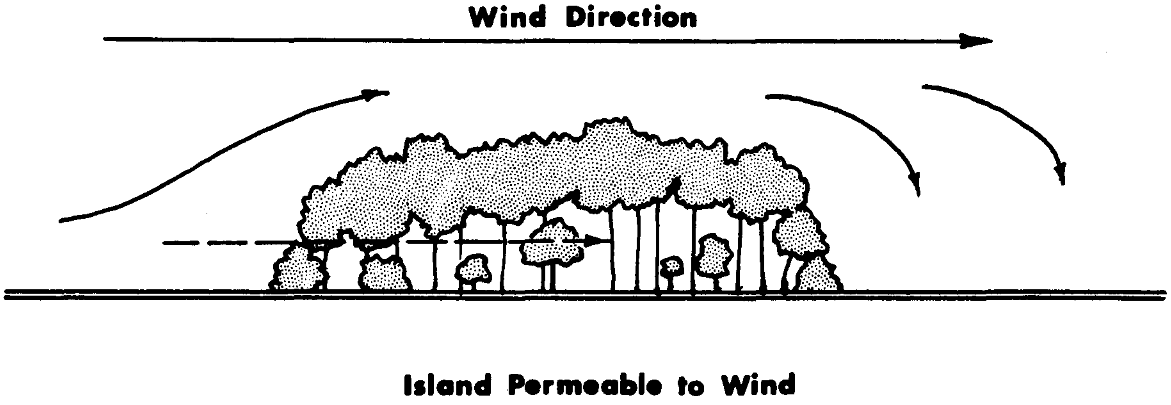

Fig. 3. Islands more permeable to air movement may cause air movement on the leeward side to change in pattern. Effects on seed dispersal by wind may be important.

wind movement around tall hedges showing that midday temperatures on leeward sides may be as much as 3°C warmer than the windward side at wind speeds of 10-20 miles per hour. This effect results from the same air circulation patterns described by Moen (1974) and Vries and Afgan (1975).

Solar Radiation

Solar radiation is perhaps the most important physical factor influencing forest edge. Its effect is controlled by edge aspect (Wales 1967, Wales 1972, Swift and Knoerr 1973) and latitude (DeWalle and McGuire 1973). Geiger (1966) demonstrated that diffuse sky radiation, which may make up 10-20 percent of the incoming radiation, acts equally on all borders but direct radiation is subject to the influence of aspect. He stated that a south facing border may receive 180-200 hours of sunshine a month in mid-summer while a north border may receive only 20-60 hours during the same period. Consequently, the warmest and driest exposures are those with southerly aspects if air movement and angle of solar incidence are not considered. Measurements by Swift and Knoerr (1973) characterized the radiation balances for varying aspects of forest slopes. Forest edges of similar aspect on level ground may have similar balances. However, direct comparisons between canopy and edge radiation loads were not made nor were atmospheric effects on solar radiation considered.

Not only direct solar radiation, but reflectivity (albedo)from adjacent fields (Lowry 1962, Lykowski 1970) contributes to the different energy balance of forest edges (Figure 4). The amount of radiation received by forest edges through reflection and re-radiation from nearby fields is dependent on the field's use. Kittredge (1948) stated that radiation from forest- and litter-covered soil is much less than from bare soil. Colwell (1974) showed that reflectivity from an open field may be 50 percent more than that of a forest.

According to Reifsnyder (1965), two-thirds of the radiation received by a forest is lost as heat through evapotranspiration with most of the rest lost through convection. Light intensity, which at times is higher on edge trees due to lateral exposure to direct and

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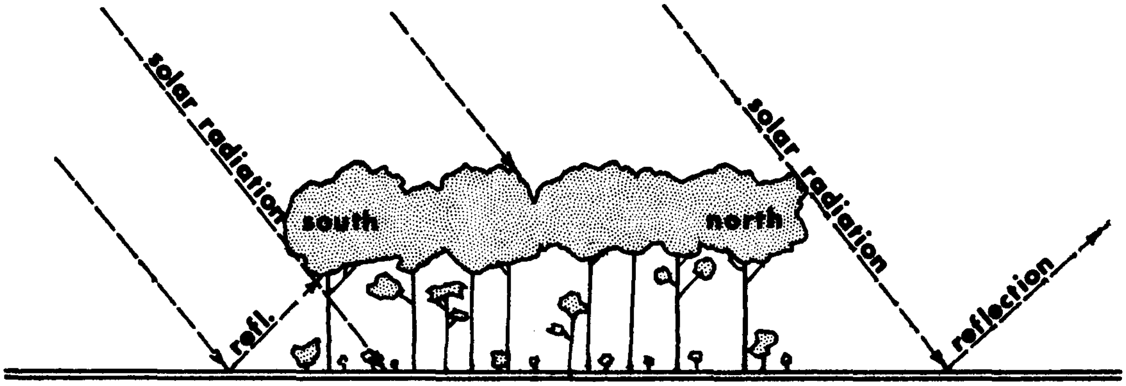

Fig. 4. Solar radiation does not affect all edge aspects equally. Northerly aspects receive almost no direct solar radiation and limited reflection from nearby fields in most parts of the United States. Southerly aspects receive much more radiation.

indirect radiation, acts to increase transpiration (Salisbury and Ross 1969, McConathy et al. 1976). One of the interesting aspects of increased edge tree exposure to wind and direct radiation is the greater importance evaporation plays in heat dissipation (McConathy et al. 1976b). Forest interior trees rely less on evaporation and proportionately more on radiation for heat dissipation. A model developed for simulating the hydrology of a terrestrial ecosystem (Huff et al. 1976) rely heavily on levels of incoming radiation and wind speed for calculating moisture loss. Applying theoretical edge conditions to the model would result in a much drier simulated environment. Studies on tree shape and theoretical energy receptivity (Jahnke and Lawrence 1965) demonstrate the importance of the vertical dimension of open-grown trees in increasing photosynthetic surface exposure to solar radiation. Implications are that open-grown trees may receive twice the energy of forest grown trees (Reifsnyder 1965). Realizing that edge trees are neither totally open- or forest-grown, the radiation they receive per individual tree is probably greater than forest-interior trees of the same stem diameter but the extent of the increase is highly dependent on edge aspect. This places a comparatively heavy load on some forest edge trees for heat dissipation (Knoerr and Murphy 1972, Gates 1965). Solar radiation was shown to be the most important factor related to tree water status in several tree species of an oak-hickory forest in Missouri (Thompson and Hinckley 1977). Geiger (1966) showed that daily maximum temperatures just above the ground surface along a forest edge are usually 11°C higher than the forest interior (Murphy et al. 1972). Kittredge (1948) demonstrated that July temperature departures of a forest from open areas occur even when expressed as mean figures (Table 1) Investigation of the adsorption of solar radiation by vegetation and plantless soil (Lykowski and Radomski 1975) shows quantitatively how direct solar radiation can affect microclimates that may resemble portions of forest edges.

Table 1. Departure of New York Forest Temperatures from open Temperatures (°C) in July (after Kittredge 1948)

Forest	Mean Maximum Temperature (C)	Mean Minimum Temperature (C)
Beech Climax	-4.6	2.5
Hemlock	-2.7	2.2
Beech-Maple	-7.1	*

*not available

The depths to which solar radiation penetrates the vertical edge of a forest (Figure 5) is dependent on the solar angle, edge aspect, and the density and height of edge vegetation. Latitude, time of year, and time of day affect solar angle. All these factors except edge vegetation height will affect radiation intensity. Reifsnyder (1965) stated that "on level ground at 40 degrees latitude, the shadow at noon on December 21 is 1.8 times the height of trees; on March 21 it it 0.8; on April 21 it is 0.5 and on June 21 it is 0.3." Light penetration into a newly created south edge then follows the same proportions with respect to the height of the live crown. More radiation is received by a south edge during the growing season both before and after the summer solstice than during the summer solstice. Figure 6 demonstrates radiation levels at noon in the fall for south edges which may receive approximately 3/4 the radiation received by the upper canopy of a forest. The total incoming radiation for various forest edge aspects by day or season has not been calculated or measured. Hutchison and Matt (1977) conducted an excellent study of seasonal radiation flux for a tulip poplar (Liriodendron tulipifera) forest. Daily incoming radiation exceeded 650 langlys per day above the canopy. Although the daily load for edges may not be as great as the canopy, during specific times of the day edge radiation loads may be greater (i.e., west aspects

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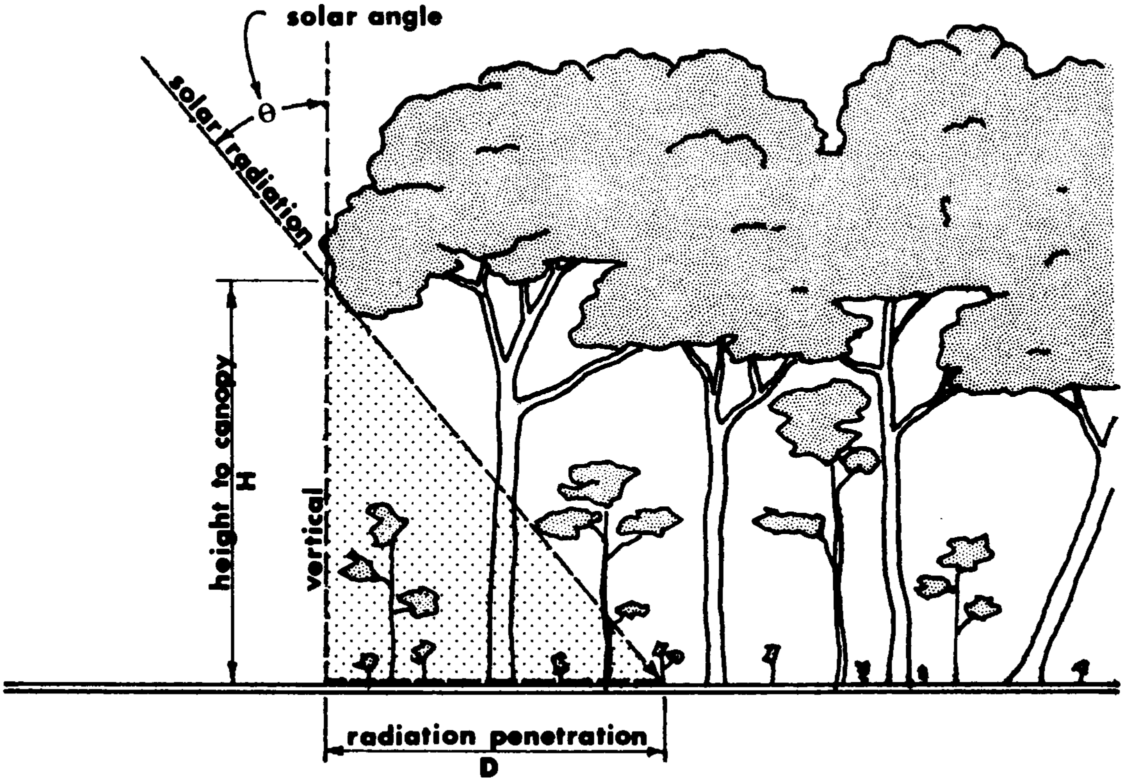

Fig. 5. The depth of solar radiation penetration into a newly created forest edge on level ground is dependent on the height of the canopy and the solar angle where the distance of radiation penetration, (D) is equal to the height of the canopy, (H) times the tangent of solar angle, (0). The solar angle is dependent on the latitude of the stand, the time of year, and the time of day. Within the zone of radiation penetration light intensities and summer daytime temperatures are higher than forest interiors sheltered by a tree canopy.

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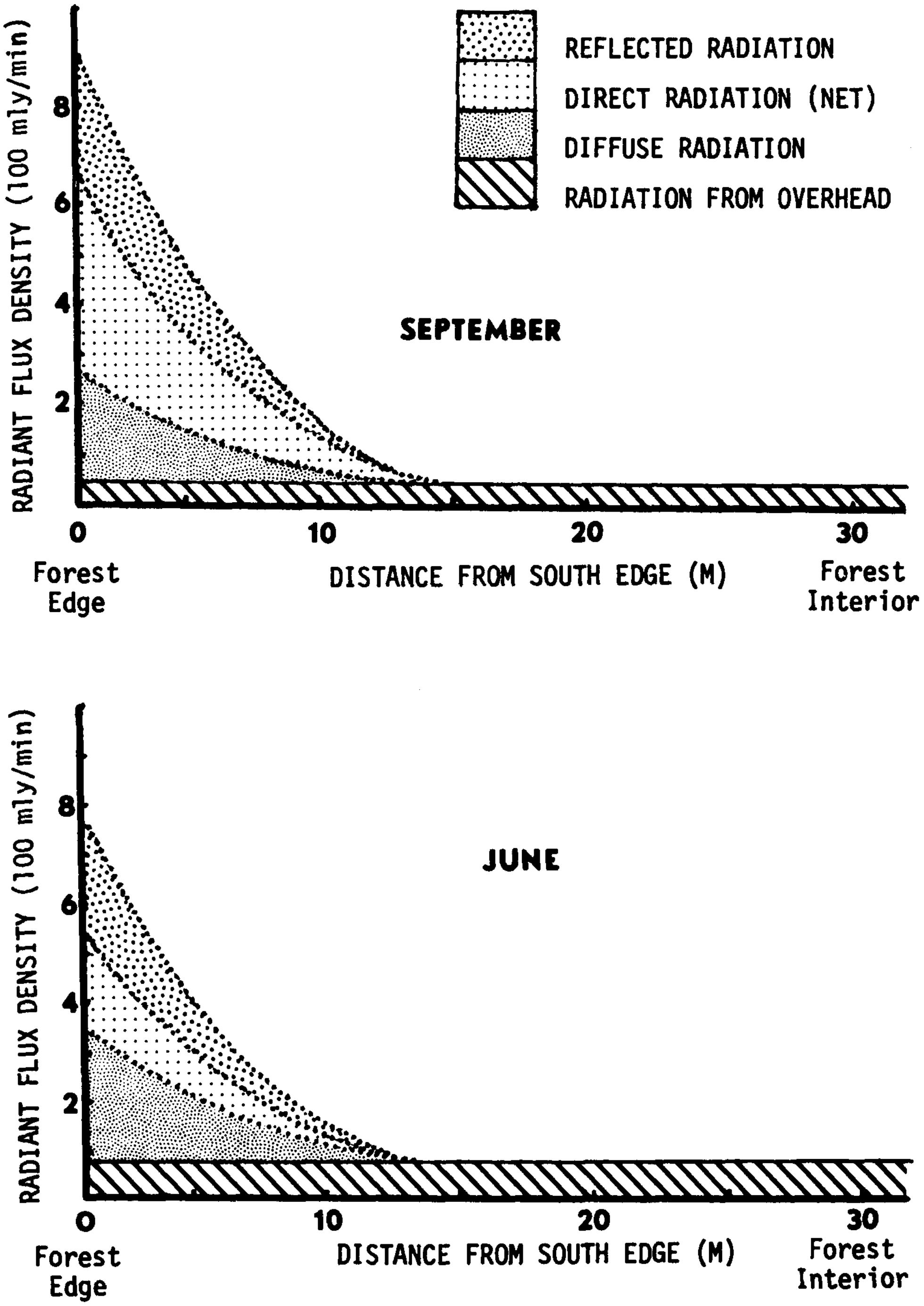

Fig. 6. Estimated incoming solar radiation levels at the forest litter on the south edge of a forest island. Information was drawn from several sources (Bruner 1977, Hutchison and Matt 1976a, Colwell 1974, Swift and Knoerr 1973, Geiger 1966, Lowry 1965, and Reifsnyder 1965).

on late afternoons in the summer). Solar incidence and reflectivity from adjacent land play an important part in edge radiation loads compared to the canopy.

Increased light intensity in newly created edges acts differentially on edge vegetation. Some species, such as beech and maple are susceptible to sun scorch (Reifsnyder 1965). McCormick (personal communication) found that bud mortality in several pine species increased as a forest edge was approached. For other species such as maple, shade tolerance appears to be a function of height (Fowells 1965). Saplings are able to persist in the shady conditions of the understory for long periods. The same species may thrive when released to become a sun-exposed canopy tree. The older dominant trees next to a newly created edge tend to survive and flourish whereas understory saplings are representatives of different, light-tolerant species (Smith 1962). Given time and a rapid response to changes in light intensity, the shade-intolerant species may eventually compete with the tolerant canopy trees. In doing so, however, light intensities are reduced in the understory and the effective edge width for understory species is reduced (Wales 1972).

Precipitation - Nutrient Cycling

Difference in precipitation along forest edges of different aspects is minimal unless storm patterns occur from a prevailing direction. During light rains, canopy throughfall may be reduced along forest edges. This may be due to greater interception along the edge (Trimble 1966, Hewlett and Nutter 1969). The amount of interception is dependent on the age and structure of the edge. Wind driven rains are likely to increase throughfall along windward forest edges above that in the interior. The accumulation of snow along shelterbelts (Vasilev 1976) has demonstrated that forest edges alter snow accumulation and distribution in a fashion similar to snow fences. Effects of snow accumulation on spring microclimate and moisture availability are believed to influence seed germination and plant growth at forest edges but research is needed to determine any definate effects.

Edge trees that have roots extending into adjacent fields are exposed to a different soil moisture regime than those in the forest interior. Precipitation interception losses of forests are greater than those of open fields. Although additional moisture reaches field soils, higher soil temperatures and wind increase evaporation (Kucera 1954) near the forest edge and negate this moisture gain (see "Wind" and "Solar Radiation" sections).

Effects of variations in throughfall distributions, litterfall, temperature and radiation on edge nutrient cycling have received some indirect attention in studies of forest interiors. Reiners (1972) investigated the input of Ca, Mg, N and P into forest stands and found that N input was highly dependent on litterfall and Mg was dependent on the amount of throughfall. All the elements tested (except phosphorus) were directly correlated with rainfall. Inferences from Swank and Douglass (1975) are that newly created forest edges may be suseptable to initial increased NO_3 loss for 10 - 20 years while returning to baseline levels after this period. Other nutrient flux measurements indicate that NH_4, Cl^-, K^+, Ca^+, and Mg^{++} is also lost while PO_4 is not affected. Eaton, Likens and Bormann (1973) stated that transpiration serves as a stabilizing mechanism for plant nutrient conservation. Higher edge transpiration rates, combined with increased litterfall at edges, may result in greater nutrient cycling, provided litter were to drop in place. However, this has not been proven. The direction of prevailing winds may affect the distribution and accumulation patterns of litter on various edge aspects.

Soil studies, such as those in McIntosh (1957), have shown pH to be lower along forest edges than interiors. His study emphasized phytosociological relationships with little reference made to abiotic gradients. Although specific studies have not been conducted to determine the cause of pH differences, five are now suggested: (1) root exudates, (2) litter type (a result of vegetation type), (3) microclimate and water infiltration rates, (4) microbial decomposition, and (5) potential combinations of these factors.

The root exudates of only a few tree species have been investigated in detail (Smith 1976). Some root exudates are acidic and the variation between species can be quite large. Species composition differences between forest edges and interiors may account for a substantial difference in soil and litter pH. This hypothesis has not been tested. Root competition effects stimulated by root exudates occur in edges as well as in forest interiors. Some species more commonly found in edges (*Juglans nigra* in southeastern Wisconsin and *Sassafras albidum* in east Tennessee) (Fowells 1965) are known to contain substances toxic to their own roots and those of other species. However, the effects of interfering root exudates along forest edges are not known. If, indeed, "edge" species cause changes in soil pH or chemical content, the effect on species composition and development could be altered from interior conditions.

The chemical composition of throughfall may be different in forest edges (Reiners 1972, Sequin 1974). The leaching and washing of leaves that differ in amount and kind from forest interiors would affect nutrient content in edge throughfall.

The processes which mineralize litter may account for differences in nutrient cycling between edges and forest interiors. Smaller stands, subjected more to the drying effects of the wind, may have a slower rate of litter decomposition (Forman 1975) and nutrient cycling compared to forest edges. Microbial composition and activity probably play an important role in the rate and qualitative mineral output of the litter decomposition process. More investigation is needed to clarify these suggested differences.

STRUCTURE OF FOREST EDGE

Forest edges at similar ages exhibit similar structure in many geographic regions. Barick (1945) was probably the first to study forest edge structure in detail and directed attention toward habitat transitions between forest types. He reported understory cover densities to be only 15 percent in forest interiors, but 40 percent along the edges. He attributed the difference to greater leaf and stem densities in the transitional regions.

Later Gysel (1951), Bray (1956), Trimble (1966), Wales (1972), and Bruner (1977) found that the structure of edge communities differed from that of forest interiors. The density and frequency of saplings in the border area was much greater than the interior, but the density and frequency of larger trees was not greatly different. The portion of the crowns of the edge trees exposed to light was greater than those of the stand interior. Gysel (1951), Forman and Elfstrom (1975) and Levenson (1976) defined an edge tree as displaying considerable clear-length on the interior (forest-grown) side of the bole and lower, more frequent branching on the exterior side accompanied by an overall lean of the bole toward the edge of the stand. Horn (1971), examining the growth adaptations of trees, found that changed lighting affected the growth form and the distribution of growth products of structural support.

Forest edge width, as defined by tree composition and structure, is dependent on several factors. Wales' (1972) findings in New Jersey showed that tree basal area in edges was significantly greater than forest interiors. He identified the extent of variability in width dimensions and structure of edges with respect to north and south aspects. Northerly edges were approximately 5-10 meters wide while southerly edges were at least double that width. These dimensions are supported by Bruner (1977). Other aspects investigated by Bruner had widths within the extremes of north and south edges. The dimensions of forest edge are affected by latitude due to the amount and angle of solar radiation. It is believed that edge width is also influenced by vegetation formations acting on lighting conditions; e.g., narrower for spruce-fir forests than northern hardwood forests (Horn 1971, personal observation).

Forest edge structure is highly dependent on the way an edge is maintained by man (Fig. 7). Gysel (1951) noticed that some edges were maintained at the outer dripline of edge canopy trees while other edges were maintained either at the base of edge canopy trees where barbed

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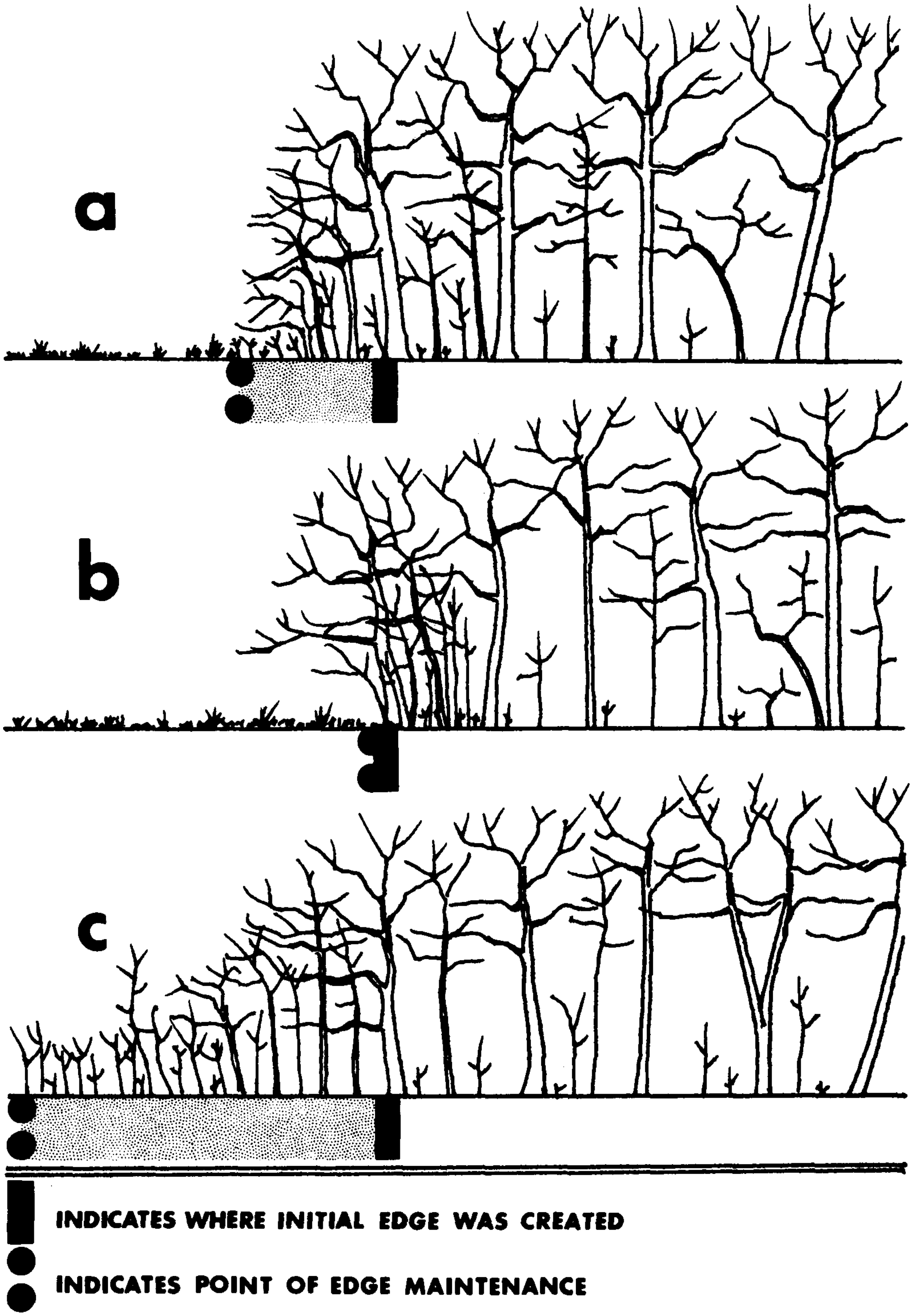

Fig. 7. Three common structures of edge are dependent on where an initial edge was created and where it has been maintained.

wire could be strung on trees, or beyond the tree dripline. This variation in edge maintenance is believed to have considerable influence on lighting conditions and wind movement within an edge which affects the way vegetation responds and develops. Kinerson and Higginbotham (1973) have simulated branch wood production and suggest that their model could be modified to accept the set of environment factors occurring at forest edges. Such a model would allow a better understanding of the effects of certain types of edge maintenance and structural development.

EDGE COMPOSITION

Forest edge tree composition is somewhat different from forest interiors. According to Gysel (1951), tree species richness of a forest's edge was higher than the same forest's interior. In a limited survey he found 40 interior species and 59 edge species; however, 38 of the interior species also occurred in edges. The conclusion is that a large portion of the interior trees are found in edges but the reverse is not true.

The additional species existing in the edge are frequently intolerant of shade and are associated with secondary succession. McIntosh (1957) successfully correlated high light intensities (and higher soil acidity) with certain tree species found predominantly in edges. Bazzaz (1975) studying old-field succession in Illinois, found that when structural diversity was highest ("high degree of vertical and horizontal heterogeneity") and most resembled edge conditions, species diversity was highest and "both shade-tolerant and shade-intolerant species (were) present together." Although edge composition seems somewhat variable, the frequency with which most species are encountered is rather high compared to some of the interior species. However, forest interiors are believed to contain a larger number of potentially rare species. Frei and Fairbrothers (1963), after studying the distribution of vascular plants in a New Jersey forest, found that of the 312 species identified, 77 percent were found in the forest interior and 57 percent occurred along forest edges. Only 13 percent of the species were trees. Forman and Elfstrom (1975) and Elfstrom (1974) observed proportional relationships between forest island size, tree species diversity, and structure. Such relationships affect the extent of contrast between forest island edges and interiors. Fox (1977), Harper (1976) and Bray (1956) have concerned themselves with gap-phase replacement and the alternation of tree species that occur in steady state communities. The species richness of forest edges and their exposure to interisland seed exchange may alter the replacement probabilities in edges and deep forest. The ultimate impact of this phenomenon on forest island composition and inter-island seed rain has not been investigated.

Several studies (Wales 1972, Weber 1975) have uncovered a propensity for forest edges of various aspects to have varying composition. However, high data variability makes the compositional distinction between edge aspects less than certain. Personal studies as well as those by Bruner (1977) substantiate the tendency toward compositional variations between aspects. Edge maintenance is often so variable in timing and quality that definite compositional trends for edge aspects are difficult to identify. Extensive field data and historical records of edge treatments, the later often not available, are needed to clarify edge aspect distinctions in composition.

COMPETITION-DEVELOPMENT WITHIN EDGES

Forest edges are dynamic and change in size, composition, and structure through time. It is not known if a terminal equilibrium stage of edge development is reached. Almost all of the edges described in the literature were less than 100 years old. Forest openings, or gaps, appear to have a structure and species composition similar to edge communities (Gysel 1951, Bray 1956, Wales 1972). A study of canopy encroachment into forest openings reported that rates of encroachment are species-dependent (Trimble 1966). Species capable of developing pronounced lateral branching (Quercus rubra) were favored slightly over those characterized by strong vertical growth

(Liriodendron tulipifera). The same principles should apply to edge trees.

Root competition for moisture and nutrients along forest edges has not been investigated. Basal area along edges was shown to be considerably higher than forest interiors in New Jersey (Wales 1972) and the same was suggested by Levenson (1976) in Wisconsin. The root system which supports this higher edge basal area is made up, at least in part, by roots extending into adjacent unforested land where deep root competition may be reduced. It is likely that the density of deep roots along an edge is not much different from interior forests since large stem basal area is about the same (Wales 1972). But density of shallow roots is believed to be much higher in edges as indicated by the high stem density of understory shrubs and saplings in Wales' data. These shallow roots intercept much of the throughfall precipitation (Auclair and Cottam 1971). Species that are able to survive high root competition and limited moisture in the early stages of growth are favored in edge habitats. Tree composition reflects this condition since many of the seedlings which occur along edges and not in forest interiors are somewhat drought resistant (Curtis 1959).

Baker (1972) discussed relationships between seed weights and drought stress in California. Xeric conditions seemed to favor larger seeds. This suggests that human influences which tend to make habitats more xeric may provide selective advantage for species with heavier seeds. Additionally, moisture availability may be a more important stress factor for trees than shading and competitive stress (Baker 1972). Harper, Lovell and Moore (1970) state that the "advantages of large reserves are offset by disadvantages in water relations, dispersibility, and predation risks," a factor of no small importance in forest edges.

Competitive advantages for light in edge development are believed to be related to the way in which vegetation responds reproductively and structurally to the creation of an edge. Two main vegetative responses are epicormic branching and root or stump sprouting. Wales (1972) noted that forest edge species were often capable of vegetative reproduction. One of the more notable examples is the sprouting response of American basswood (Tilia americana). Although basswood will produce stump sprouts in interior forests (Curtis 1959), the species appeared in greater numbers as sprouts at the base of living and dead basswoods directly adjacent to edges (personal observation). Consideration of basswood's autecology seems to suggest that basswood is not an "edge" species. Its prolific sprouting on edges is believed to be an expression of crown stress or environmental stress. This is substantiated by the great amount of basswood mortality along older forest edges (personal observation). American beech (Fagus grandifolia) can produce prolific root sprouts but generally occurs at lower basal area (and not as sprouts) along edges compared to interior statistics (personal observation). Thus, the capability of sprouting in itself does not insure advantages in forest edge competition for light.

Disturbed areas usually have a high proportion of bird and animal dispersed species (Auclair and Cottam 1971, McBride 1973, Howe 1975, Smith 1976). I have observed similar patterns in edge communities. The edges examined, generally under 100 years old, are well stocked with disturbance species in the understory. The genera Prunus, Crataegus, Quercus, Carya, Cornus, and Populus, other members of the Rosaceae, and the Caprifoliaceae are well represented.

Whether forest succession along forest edges progresses as it does in larger forest stands has not been discussed in the literature. Consequently, the changes in species composition that occur in an edge through time may or may not stabilize. Clements (1916) discusses man-maintained disclimaxes where forest composition is held consistently short of a given climax composition. The same may be true for forest edges where influences of cleared land act to continually maintain pioneer conditions (Curtis 1956, Auclair and Cottam 1971, Levenson 1976).

Studies which identify stable tree communities in forests seem to indicate that, based on species composition and size-class distribution, no edges examined in the selected literature were in a steady state. The basis for this is that Bray (1956) and Zedler and Goff (1973) defined a stable plant community (climax) "as one having individuals of the dominant species present in all size classes." This means that the edges examined were either not yet stabilized, or if they were, they could not be described using conventional definitions of compositional stability.

The results of studies by Barick (1950), Gysel (1951) and Wales (1972) should be considered with respect to a larger dynamic landscape in which new edges are being created and old ones destroyed (Levin and Paine 1974, Johnson and Sharpe 1976). The edges that have been studied probably do not represent the range of edge ages and conditions which exist in a region. Generally those edges studied had distinct linear borders and were not less than about 40 years old. However, many regions contain less distinct wavy edge boundaries of varying ages which make up a significant proportion of a region's edge communities.

EFFECTS OF PRIMARY CONSUMPTION IN FOREST EDGE

Consumption of propagules in forest edges may at times account for 100 percent of the mortality of nuts, seeds and seedlings (Howe 1975, Smith 1975). Such effects, however, are offset by occasional years of high seed production by certain tree species. During such years, propagule mortality from consumption is not complete and may be accompanied by increased caching (States 1976). Wall and Balda (1977) found that during years of high propagule production certain bird species will disperse and cache quantities of propagules that exceed over-wintering requirements by 2.2 to 3.3 times. In addition, predominantly viable seeds were collected and cached. The excess propagules may wind up being consumed by other animals or they may decay or germinate. High nut, fruit, and seed production by individual trees has been shown to result in increased consumption, dispersal, or caching of those propagules (Wall and Balda 1977, Howe and Primack 1975). Ghiselin (1977) suggests that there are also more animal species in edges where primary productivity is high inferring that there may be more efficient predation (or dispersal) of tree propagules. Sork and Boucher (1977) studied the production, predation, and dispersal of hickory (Carya glabra, Mill. sweet var. odorata) in southeastern Michigan and concluded that the number of nuts "removed" varied directly with the number available, the rate of removal increasing with the increased number of viable fallen nuts. The relationships of high edge primary productivity with propagule production and, in turn, propagule predation, dispersal, and caching are not yet well understood. Forest edges are assumed to produce more propagules per unit area than deep forests on the basis of substantiated higher edge primary productivity. If so, the propagules of edge trees would have a higher probability of dispersal and caching between forest islands than interior trees year in and year out. Sork and Boucher found this not to be true when studying individual trees; the probability of removal remained constant per nut per week for hickories. However, as more nuts were present, a proportionate number were removed (dispersed or cached). Many small mammals utilize edges as corridors for movement and foraging (Ghiselin 1977). Foraging patterns develop which utilize food resources in and near edges in preference to more distant sources (Smith and Aldous 1947, MacFadyen 1957, Van Winkle et al. 1973, Schreiber 1976, States 1976). Rabbits and squirrels have been known to rely on the great density of young stems in edges as a food source (debarking) during lean food years. Barick (1950) commented that the effects of browsing by deer is an important impact of forest edge. Deer may consume enough shoots and twigs to create a browse line.

There may be a marked difference between animal predation on plants, seed consumption, propagule caching and seed excretion by birds and animals for many tree species when comparing forest edges to forest interiors (Carpenter 1935). Although the extent of the difference is statistically untested, propagule invasion rates and their survival to reproductive maturity is of considerable importance to forest development (Hett and Loucks 1971, Holt 1972). Of mammalian consumers and dispersers of hickory nuts, beechnuts, walnuts, and acorns, the most important is the gray squirrel (Sciurus carolinensis). However, the red squirrel (Tamiasciurus hudsonicus), fox squirrel (Sciurus niger), flying squirrel (Glaucomys volans), eastern chipmunk (Tamias striatus), and small rodents such as Peromyscus leucopus are known to prey on nuts (Sork and Boucher 1977). Attempts at modeling seed dispersal by animals (DeAngelis, et al. 1977, Bullock and Primack 1977) are beginning to appear in the literature and present a useful way of understanding some of the inter-relationships between trees and animals.

POSSIBLE EFFECTS OF EDGE ON FOREST DEVELOPMENT

Forest edges are compositionally different from forest interiors and are more exposed to propagule vectors (wind and many animals) than forest interiors. Their contribution to, and effect on, the reservoir of propagules dispersed between isolated forest stands may be substantial. The inter-island seed reservoir has already been depleted in some landscapes as a result of a reduction of propagule sources. Clements (1916) noticed this in the region around the Missouri River and Gomez-Pompa et al. (1972) noticed similar conditions in the tropics. Auclair Cottam (1971) discussed the highly localized distribution of sugar maple (Acer saccharum) and its inability to disseminate propagules to distant stands in south central Wisconsin.

Plants have often been thought to "saturate the surrounding environment with progeny" (Salisbury 1942) but this apparently does not hold true for many regions. When land is extensively cleared of original forests, proportionately more area in edges is created, i.e., the ratio of edge area to interior area increases (Curtis 1956, Levenson 1976). In such landscapes, forest edges, with their high exposure to propagule dispersal vectors, may contribute an important component to the declining propagule supply available for inter-stand transport. This disproportionate contribution of propagules by forest edges (based on forest area) may eventually affect propagule invasion rates and ultimately the species composition of isolated forest stands (MacArthur and Wilson 1967).

The concepts of island biogeography may cautiously be applied to such situations (Levins and Culver 1971). Diamond (1975) notes some formerly continuous natural habitats have been reduced to disjunctive pieces not unlike small island archipelagoes. He further states that "for a forest species, a wooded tract is a distributional island surrounded by a sea of non-forested habitat..."

Important variables in dissected landscapes are distances between forest islands, the amount of forest edge (which is related to forest stand size and shape), the dispersal characteristics of the tree species involved, the arrangement of forest islands and the normal sequences in succession (MacArthur and Wilson 1967, Cromartie 1975). McIntosh (1957) suggests that vegetation in a region may contain several alternative but parallel avenues of succession. Changes in propagule invasion rates could favor one avenue of succession over another causing a shift in the composition of forests on a regional basis (Curtis 1956, Auclair and Cottam 1971). A study of seed dispersal changes of annuals and small perennials showed that a stable population size was a function of dispersal and reproductive capacity (Bullock 1976). If the same principles apply to arboreal species, increased distance barriers to seed dispersal would mean a change in stable population sizes.

The logistics of seed dispersal and spatial patterns of forests may be more critical than the direct analysis of landscape patterns would lead us to believe. Forest edges as discussed by Levenson (1976) surround a forest stand, and smaller stands are potentially composed entirely of edge. This could be an important consideration in propagule dispersal efficiency and in the arrangement of "safe sites" (Harper et al. 1961) for propagules of certain tree species within a given landscape. For example, the propagules of interior tree species would not have an equal opportunity of establishment within an entire forest stand but would be somewhat restricted to a smaller core area that excludes edge.

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