THE BOTANICAL REVIEW

VOL. 59 OCTOBER–DECEMBER, 1993 NO. 4

Tree Invasion and Establishment in Old Fields at Hutcheson Memorial Forest

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The Botanical Review 59(4): 251–272, Oct.–Dec., 1993

I. Abstract

In this review I present results from pattern analysis and field experiments in New Jersey, United States concerning tree invasion and establishment in old fields. Hutcheson Memorial Forest Center (HMF) is the New Jersey study site and a logical choice to anchor a review of this topic. HMF contains the longest and largest old field permanent plot study in the USA including extensive data concerning tree invasion and establishment. HMF has also been the site of considerable old field tree experimental research. In addition, I review other investigations of old field tree invasion and establishment of the eastern deciduous biome and contrast them with HMF. I identify critical questions concerning tree invasion and establishment, indicate what progress has been made towards answering these questions and propose future experimentation. I also synthesize results into a conceptual model and investigate the relative importance of seed and seedling processes in determining tree dynamics in old fields.

The idea of a possibility or "window" for tree invasion and establishment and its variation form the basis for this review. For example, the temporal variation of windows is reflected in tree establishment patterns at HMF because wind- and bird-dispersed species invaded one year after cessation of cultivation while mammal-dispersed species were not present until year 12. Although analysis of size classes of individual HMF trees imply that windows close quickly, studies are of too short duration to tell definitely. Spatial variation in invasion and establishment pattern includes exponential decline in seed and stem density with distance from forest edge which deteriorates with time as the old field becomes more structurally complex. Additional spatial heterogeneity occurs when seeds and seedlings of bird-dispersed species clump which conversely becomes more pronounced with time. Many of these HMF patterns are seen in other eastern United States old field sites.

When reviewing field experiments from my site and others, I focus on the spatial and temporal variation and the difference between species in the effect of processes on tree seeds and seedlings. I do this because this variation relates directly to the dynamic nature of windows whose quantification is necessary for modeling. Combining my pattern analysis with a survey of variation in seed and seedling mortality caused by different successional processes in old fields, I conclude that seed dispersal, conditions necessary for seed germination and seed and seedling predation are the critical processes controlling and constraining tree invasion and establishment in old fields. Competition and indirect effects of litter and the environment, which modify how these processes affect tree dynamics, are also important. Therefore, processes involving the interaction of species with the environment and with other species form the principal filters on and limitations to tree invasion and establishment and not the non-interactive life-history traits of individual tree species such as growth rate or longevity. The interaction of pattern and process and the affect of many of these processes on old field community structure are also discussed.

Resumen

En este estudio presento los resultados de análisis de patrones y experimentos de campo en New Jersey, Estados Unidos relacionados con la invasión y establecimiento de árboles en campos abandonados. Hutcheson Memorial Forest Center (HMF) en New Jersey es una alternativa lógica para desarrollar este tópico. HMF contiene el area de estudios relacionados con el monitoreo de vegetación en campos abandondos más grande y de más larga historia. HMF también ha sido el sitio de investigación de arboles en campos abandonados por décadas. También estudie otras investigaciones de invasión y establecimiento de arboles en campos abandonados en un bioma forestal del este y los comparé con los de HMF. Identifico preguntas críticas sobre la invasión y establecimiento de árboles, indico cual es el progreso hecho en contestarlas y propongo experimentos futuros. Finalmente, yo sintetizo los resultados en un modelo conceptual e investigo el papel que juegan los procesos a nivel de semillas y plántulas en la dinámica de arboles en los campos abandonados.

Las ideas de la oportunidad de una invasión y establecimiento de árboles y su tiempo de invasión forman la base para este estudio. Por ejemplo, la variedad del tiempo de invasión se refleja en los patrones de establecimiento de los arboles en HMF. Porque las especies de arboles dispersadas por el viento y aves invadieron un ano despues de la cosecha mientras que las especies dispersadas por mamiferos invadieron despues 12 anos. Aunque el análisis de los tamanos de los árboles en HMF implica que la oportunidad de invasión no dura mucho, es to no se puede con cluir ya que los estudios fueron de muy corta duración. La variación espacial en el patrón de invasión y establecimiento de los arboles tiene una reducción exponencial en la densidad de semillas y tallos de donde termina el bosque. Esta reducción se desvanece según la estructura del campo abandonado se complica can el tiempo. En contraste, un patrón espacial que se hace mas aparente con el tiempo es el amontonamiento de semillas y plántulas dispersas por aves. Muchos de estos patrones son observados en otros campos abandonados en el este de Estados Unidos.

Cuando reviso los experimentos en el campo de HMF y de otros lugares, enfoco el efecto que tienen la variedad en tiempo y espacio de la invasión y la diferencia entre las especies de árboles en los proceso a nivel de semillas y plántulas. Esta variedad se relaciona directamente con la naturaleza dinámica de las oportunidades de invasión cuya cuantificación es necesaria para hacer el modelo. Combiné mi análisis de los patrones con un estudio de variación en la mortalidad de las semillas y plántulas causadas por diferentes procesos sucesivos en campos abandonados. Concluí que la dispersión de semillas, las condiciones críticas para la germinación de semillas y el consumo de semillas y plántulas son los procesos críticos que controlan la invasión y establecimiento de árboles en los campos abandonados. La competencia entre plantas y los efectos indirectos del ambiente y de la capa de vegetación muerta en el suelo, modifican cómo los procesos de dispersión, germinación y consumo afectan la dinámica de los árboles. Por lo tanto, son las interacciones de las especies con el ambiente u otras especies las que controlan la invasión y establecimiento de árboles y no las características de las diferentes especies tales como el incremento en crecimiento o longetividad. Las interacciones de patrones y procesos con la estructura de la comunidad en campos abandonados estan discutidos también.

II. Introduction

Trees reinvade and reestablish eastern deciduous forested areas after extensive human disturbance (Finegan, 1984). These disturbances include clearcuts (Alexander, 1969; Frank & Safford, 1970; Gholz et al., 1985), right-of-ways (Canham & Wood, 1988; Hill & Canham, 1989; McDonnell & Koch, 1990; Putz & Canham, 1990) and agriculture (Bard, 1952; Bazzaz, 1968; Canham & Hill, 1990; Myster & Pickett, 1992a; Oosting, 1942). The study of tree regeneration after disturbance may enhance our understanding of more natural transitions from grassland or meadow to forest and how communities can fluctuate or remain stable. In addition, after these studies we may be better able to predict and manipulate the precise nature of recovery and to better manage lands on which we desire woody vegetation (e.g. reforestation, surface mine reclamation, erosion control, wildlife habitat, parks and nurseries) or on those we do not (e.g. pastures, rangeland, roadsides and utility corridors, Burton, 1989). Furthermore, tree regeneration in forested areas provides a framework to compare and evaluate the validity of holistic and reductionistic theories of succession (Finegan, 1984).

Much of tree regeneration after forest disturbance comes from root and stump sprouting of cut trees or from seedlings/saplings established prior to the disturbance (e.g. clearcuts and right-of-ways; Fowells, 1965). Only in minespoils and areas abandoned after agriculture (i.e. old fields) however, do trees regenerate after complete destruction of the natural vegetation where no stumps, seedlings or woody remnants of any kind remain. Consequently, old fields represent a more extensive recovery process in comparison to many other forest successions. In old fields we have the ability to investigate tree seed (invasion) and seedling (establishment) regeneration in previously forested areas directly without the added complexity of stump sprouting and other modes of advanced regeneration. Thus old field experiments may advance understanding of tree seed and seedling dynamics following other forest disturbances.

Understanding succession must include understanding the dynamics of invasion and establishment (Gleason, 1927; Johnstone, 1988; McDonnell & Stiles, 1983; Pickett et al., 1987; Pickett & McDonnell, 1989) because succession usually includes a change in species composition and processes operating during succession influence species change (Drury & Nisbet, 1973; Johnstone, 1988; Miles, 1979; Pickett, 1976). Invasion and establishment are functions of the availability of safe sites (Harper, 1977) and may begin with the removal of a barrier that had previously excluded a species from a site (Johnstone, 1988). Therefore, succession largely depends on the type of barrier and the dispersion of safe sites in space and time (Noble & Slatyer, 1980). These dynamics are formalized in the concept of a "window" (Gross, 1980, Rankin & Pickett, 1989) which represents regeneration opportunities and probabilities. Windows differ between species and have spatial and temporal variation (Rankin & Pickett, 1989). Mechanistic processes affect regeneration probabilities (Connell & Slayter, 1977; Rankin & Pickett, 1989), change windows and help drive succession.

Invasion and establishment of old fields by the structurally and compositionally dominant woody species (Bard, 1952; Pickett, 1982), which include trees that are functionally significant throughout succession (Hanson et al., 1969; McDonnell & Stiles, 1983; Whitford & Whitford, 1978), has been an important part of every major investigation of old field succession in the eastern deciduous forest biome (Bazzaz, 1968; Beckwith, 1954; Buell et al., 1971; Crafton & Wells, 1934; Drew, 1942; Oosting, 1942; Pickett, 1982). Researchers have been curious about the slow rate of invasion and establishment of old fields by trees and the lack of trees in early succession and, thus, interested in the processes limiting tree regeneration (Bormann, 1953; Buell et al., 1971; Egler, 1954; Finegan, 1984; Werner & Harbeck, 1982). While these processes could be non-interactive with individual life-history traits such as growth rate and longevity dominant (the initial floristic composition; Egler, 1954, or tolerance model of succession; Connell & Slatyer, 1977; Finegan, 1984; Pickett et.

al., 1987), this is unlikely (but see Myster & Pickett, 1988 for a discussion of herbaceous species) because the potential growth rates of successional trees are certainly faster (Fowells, 1965; Grime, 1979) than the decades it takes for trees to dominate old fields in the eastern deciduous forest biome (Bazzaz, 1968; Buell et al., 1971; Tilman, 1988). Therefore, processes of interaction with the abiotic and biotic environment (e.g. dispersal, predation, competition) greatly influence tree succession and constrain tree invasion and establishment. Consequently, I will review results from interactive field experiments in New Jersey and other old field experiment sites in the eastern deciduous biome, attempt to identify critical filters to old field tree regeneration and address these questions:

(1) When do various tree species successfully invade and establish in old field succession and what is the spatial pattern of this invasion?

(2) What is the role and spatial/temporal variation in effect of these four interactive processes:

(a) dispersal
(b) factors limiting seed survival
(c) germination
(d) factors limiting seedling growth and survival

(3) Are there any indirect effects (e.g. with litter) that change the nature of these processes and do seasonal changes and yearly environmental cycles (e.g. drought) mediate these interactions?

Old field tree research at the study site, Hutcheson Memorial Forest Center (HMF), has emphasized regeneration, invasion and establishment by focusing experimentally on seeds and seedlings. HMF is located in Somerset County, New Jersey, United States (40° 30′N, 74° 34′W) and the old-growth forest has a *Quercus - Carya* canopy and a *Cornus florida* understory (Bard, 1952). HMF is important among old field research sites because of the length of time (over three decades) agricultural fields have been abandoned and tree dynamics studied there, the large number of researchers involved in these studies (Bard, 1952; Buell et al., 1971; Facelli & Pickett, 1989, 1991; McCarthy & Facelli, 1990; Meadows, 1988; Meadows et al., 1989; McDonnell & Buell, 1984; McDonnell & Stiles, 1983; Myster & McCarthy, 1989; Myster & Pickett, 1992a, b, 1993; Pickett, 1982; Rankin, 1981; Rankin & Pickett, 1989) and the existence and continuing sampling of the Buell succession study (BSS; Fig. 1; Buell et al., 1971). The BSS is the largest (10 old fields between 0.34 ha and 0.76 ha with 48 permanent plots in each) and longest (sampled from 1958 to the present) old field succession study in the United States (Myster & Pickett, 1989). The BSS data is the largest set of permanent plot measurements available concerning tree invasion and establishment in the United States. It consists of percent cover and stem density of trees identified to species in all 480 $1 m^2$ permanent plots. A test of Egler's (1954) initial floristic composition model using tree seedlings and speculation concerning the mechanisms of tree invasion and establishment were the major motivations for the BSS (Buell et al., 1971).

III. Pattern of Tree Invasion and Establishment

In New Jersey old fields, woody species richness, cover and biomass increase with successional time and exceed herbaceous species about 20 years after abandonment

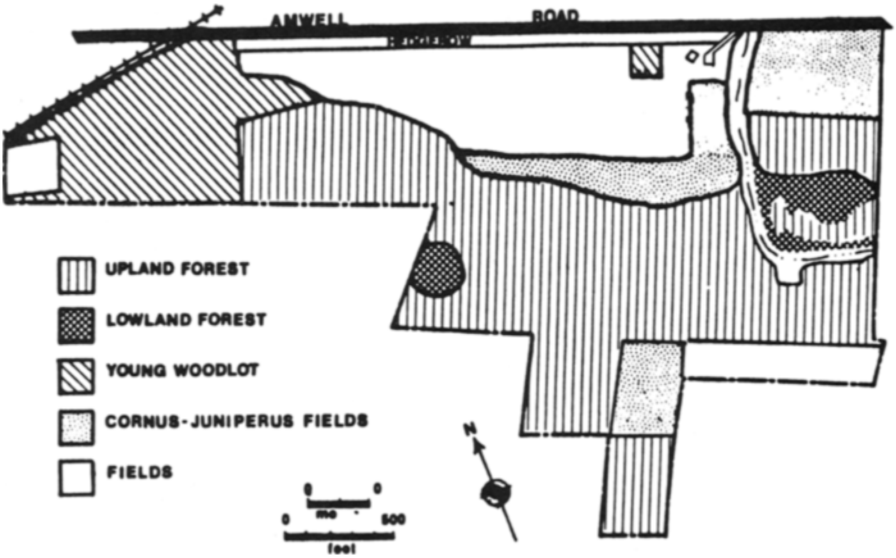

Fig. 1. Map of Hutcheson Memorial Forest Center. The ten old fields of the BSS are labeled *Cornus–Juniperus* fields in the northeast corner of the forest (used with permission of the Bulletin of the Torrey Botanical Club).

(Bard, 1952; Pickett, 1982). Functional dominance including shading and root spread (Pickett, 1982) of woody species probably occurs earlier (McDonnell & Stiles, 1983). In addition, woody individuals may exhibit more complex branching to reduce mutual shading, more planar leaf displays to intercept zenith light and higher proportions of biomass devoted to wood as succession proceeds and old fields become more like a forest (Pickett & Kempf, 1980).

Tree regeneration dynamics in old fields exhibit interesting patterns in both time and space. The temporal pattern includes when tree species invade and establish, how long they are present and their population age and size structure. The spatial pattern of tree establishment includes the degree of clustering and forest edge effects on density and composition. In the BSS fields, both kinds of patterns show window dynamics. Temporal window variation is shown by no tree establishment in year 1, followed by *Cornus florida*, *Ailanthus altissima*, *Acer rubrum* and *Juniperus virginiana* establishment in years 2–4. *Fraxinus americana* appears in years 3–4 and *Pyrus malus* in years 4–6. By the fifth year, the structure of BSS old fields changes when trees grow above the herbaceous layer and are used as bird perches (McDonnell & Stiles, 1983). *Morus alba*, *Ulmus americana* and *Prunus avium* are present in years 6–8 but stems of mammal-dispersed species are not present until the 13th year of succession (Buell et. al, 1971; Myster & Pickett, 1992a). Population size structure analysis shows that most *Acer rubrum* and *Fraxinus americana* individuals invade in the first 7 years after abandonment at HMF (Rankin & Pickett, 1989) and invasion windows may close early for these wind-dispersed trees (Buell et al., 1971; Rankin & Pickett, 1989). Alternatively, *Carya* spp., *Quercus* spp., *Ulmus americana* and *Prunus serotina* individuals invade after the seventh year at HMF (Rankin & Pickett, 1989), which is more common for trees in old fields (Bard, 1952; Pickett, 1982; Werner & Harbeck, 1982). There is generally a high turnover of tree seedlings in old fields (Buell et al., 1971; De Steven, 1991b; Myster & Pickett, 1992a), which shows the dynamic nature of windows.

Spatial window variation is shown by BSS tree stem density decreasing exponentially with distance from the forest edge early in succession. With time, this strong association with the forest edge decreases and there is an increase in significant clumping of bird-dispersed tree stems (Myster & Pickett, 1992a). In other HMF old fields, young *Fraxinus americana* saplings clump around stems of older *Acer rubrum* saplings (Rankin & Pickett, 1989). These spatial patterns may affect later composition and structure of the developing forest and persist throughout later stages of development (Hughes & Fahey, 1989, Myster & Pickett, 1992a).

Many temporal tree establishment patterns common to old field sites concur with HMF tree patterns. These include wind- and bird- dispersed species invading early and mammal-dispersed species invading later in succession (Table I). For example, the bird-dispersed species *Juniperus virginiana* is a common invader and dominates the appearance of many early successions (Bard, 1952; Lutz, 1928; Olmsted, 1937; Quarterman, 1957). Tree establishment usually does not occur immediately after abandonment and may increase with time (Bard, 1952; Werner & Harbeck, 1982). However, old field studies are not of sufficient duration or contain fields of adequate age to answer the question of length of stay, year of decline or time of departure of species (Johnstone, 1988). Therefore, studies have generally not determined the time of closing of windows for tree species (but see Rankin & Pickett, 1989). The spatial pattern of invasion and establishment at sites other than HMF includes heavy-seeded mammal-dispersed trees (e.g. *Quercus* and *Carya*) invading at the old field-forest border and lighter-seeded wind-dispersed trees, e.g. *Acer*, *Fraxinus* or *Ulmus*, developing in many areas of an old field (Drew, 1942; Lutz, 1928).

IV. Processes Influencing Tree Invasion and Establishment

Processes that determine how late successional species (e.g. trees) appear in a successional sere are of great interest to researchers of vegetation dynamics (see reviews by Connell & Slatyer, 1977; Drury & Nisbet, 1973; Horn, 1974; McCormick, 1968; McIntosh, 1980). To help conceptualize tree invasion and establishment in old fields, I represent seed (invasion) and seedling (establishment) dynamics as system states (boxes in Fig. 2) and processes (arrows in Fig. 2) in a diagram that flows downward as succession proceeds. Windows are opened by the dispersal process that adds seeds to the system. Invasion can be limited and windows closed by processes that subtract seeds from the system (arrows flowing from the invasion system state). The germination process can maintain windows by keeping some individuals viable while closing windows for others when germination does not occur. Likewise, establishment windows can be closed or narrowed by processes that subtract or limit the growth of individuals (arrows flowing from the establishment system state). Windows change under the influence of successional processes which represent changes in the probabilities of invasion and establishment. For example, plant-plant competition changes windows in an old field system. For Beckwith (1954), the last cultivated crop persisted after abandonment and competed with woody species trying to regenerate. The last crop slowed tree regeneration, reduced probabilities and

Table I

Tree genera and the year of their establishment in old fields studied in the eastern deciduous forest biome.

State	1–10	10–20	20–30	30–40	40+	Reference
Conn.	J, B A, Co					Lutz 1928
Minn.	P, B					Stallard 1929
Conn.	P, J		A, Q, B			Olmsted 1937
Misso.	D, S Q, Ca					Drew 1942
N.C.	P	Co	Q	B, J A, N	U, D Ca	Oosting 1942
Wis.		P, U		Q, P		Thompson 1943
Lou.		D, Q				Bonck and Penfound 1945
N.J.	J, A Co, P	Q, Ca				Bard 1952
Mich.		M, P	Q, F, T A, Ca			Beckwith 1954
Vir.	U, Ca	Q, L, D	P, Co			Byrd 1956
Tenn.	U, Ce	J, F	Q, D, J	M		Quarterman 1957
Ill.		D, S, U	J, Q	Ca		Bazzaz 1968

A:Acer, B:Betula, Ca:Carya, Ce:Celtis, Co:Cornus, D:Diospros, Fa:Fagus, F:Fraxinus, J:Juniperus, L:Liguidambar, M:Morus, N:Nyssa, O:Oxydendren, P:Pinus, Q:Quercus, S:Sassafras, U:Ulmus

narrowed establishment windows through competition. Therefore, windows are dynamic, differ between tree species and show spatial and temporal variation during old field succession. The general causes of succession are here represented as old field abandonment (site availability), tree seed dispersal (differential species availability) and seed and seedling processes (differential species performance; Pickett et al., 1987). The time scale for tree invasion and establishment is the early years of succession but may extend further in patches where invasion and establishment opportunities still exist (Rankin & Pickett, 1989).

A. OLD FIELD ABANDONMENT

Old fields are abandoned with a variety of initial conditions which may potentially affect tree invasion and establishment. These factors include the year of abandonment, season of abandonment, percent of border with forest, last crop planted in field (Bazzaz, 1968) and whether fields were plowed under or left fallow when abandoned (Myster & Pickett, 1990). The relationship between season of abandonment and when tree seeds mature, are dispersed and germinate has been thought to be important in determining invasion and establishment patterns (Keever, 1979). However, the BSS data suggests that the nature of the persisting last crop is critical because it competes with tree seedlings and reduces tree regeneration (*Dactylis glomerata* for HMF; Myster & Pickett, 1988; Myster & Pickett, 1990). The relationship between other old field initial conditions and tree invasion and establishment needs further investigation.

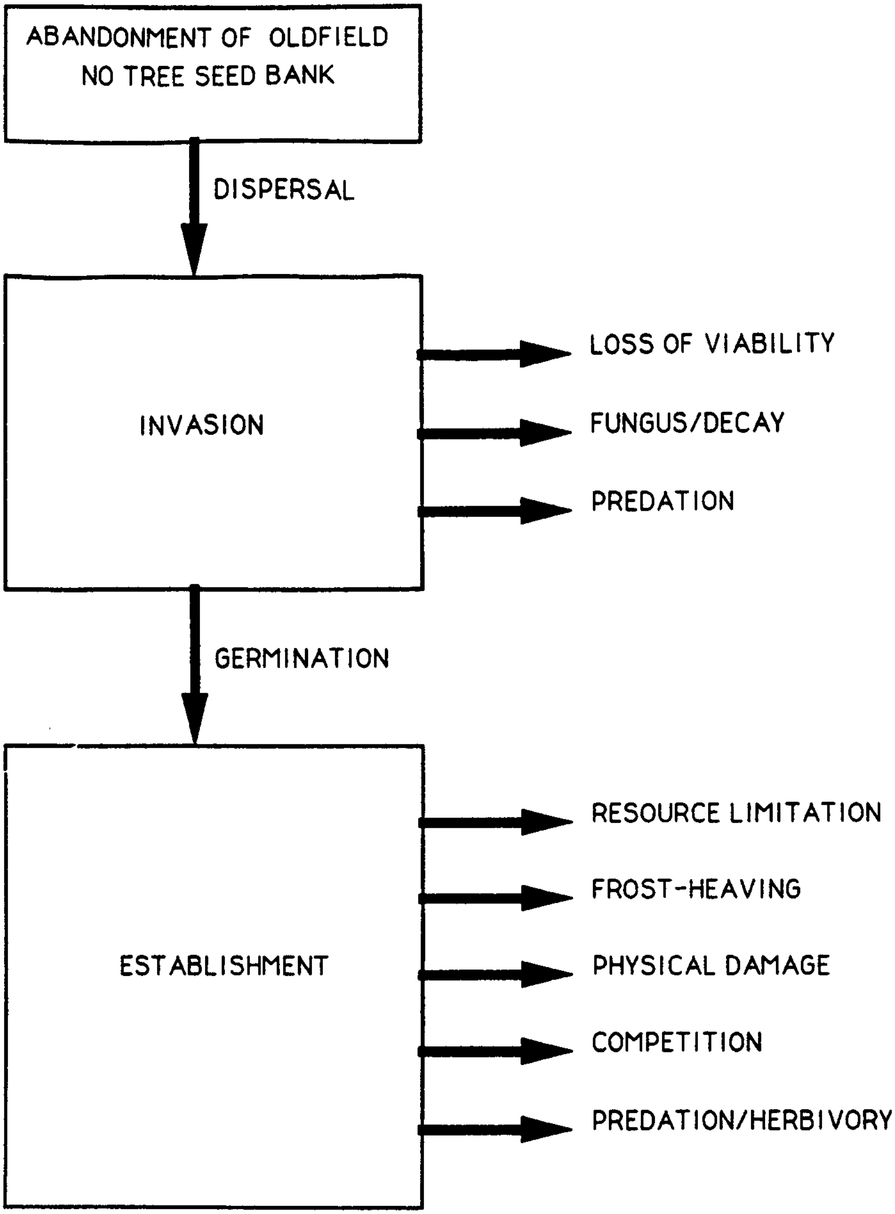

Fig. 2. Demographic conceptual model of tree invasion and establishment in old fields, contrasting the processes that add tree seeds (dispersal) and tree seedlings (germination) to the old field ecosystem (indicated by down arrows) against the processes that subtract them through mortality (indicated by side arrows).

B. TREE SEED DISPERSAL

Tree propagules are added to the system through dispersal (Myster & Pickett, 1992a) and therefore, dispersal is the only process that can open windows. Because most establishment occurs within a few decades after abandonment (Rankin & Pickett, 1989), dispersal is probably from outside an old field even through a few trees in the old field may mature and produce seed within this time (Bazzaz, 1968). HMF tree seeds have a exponential decline of seed density from the forest edge. There are 4 times (770 total seeds for a density of 53.2 per m^2) more bird-dispersed seeds in a structurally complex 13 year field with saplings above the herbaceous layer compared to a 3 year field (208 total seeds for a density of 7.4 per m^2) which implies that these perches serve as recruitment foci for bird-dispersed species. Also in a 13 year field, *Juniperus virginiana* seed was 64.7% and *Cornus florida* seed was 11.3% of the total seed input, and in the 3 year field, *Juniperus* was only 12% and *Cornus* seed input minimal. Seed input under saplings increases proportionally with sapling height but there is a critical height under which birds ignore saplings (McDonnell & Stiles, 1983). Wind-dispersed seed densities are probably similar to bird-dispersed densities (McDonnell & Stiles, 1983), but mammal-dispersed seed may be absent till later in succession (Myster & Pickett, 1992a). These patterns generally agree with the seed rain density measured under established trees in Illinois old fields (Burton, 1989).

The critical importance of dispersal on the pattern of tree invasion and establishment is widely supported in observational studies (Barnes, 1966; Bazzaz, 1968; Debussche et al., 1980; Gifford, 1966; Hughes & Fahey, 1988; Werner & Harbeck, 1982). For example, the invasion and establishment of pines on the Piedmont of North Carolina depends on the proximity of pine seed source, the pine seed year (Oosting, 1942) and the greater mobility of pine seed (Billings, 1938; Bormann, 1953; Coile, 1940) and in Georgia, bird dispersal enhances sweet gum invasion (Billings, 1938; Bormann, 1953). Tree establishment is related to availability of seed source, distance to seed source and quality of seed year (Beckwith, 1954; McQuilken, 1940). In addition, there is greater effectiveness of establishment when the seed source or forest is on more than one side of the field (McQuilken, 1940).

This close relationship between dispersal and establishment was confirmed in my analysis of the pattern of invasion and establishment in the BSS (Myster & Pickett, 1992a). Dispersal was implicated in affecting establishment and the significance of distance to seed source in the old growth forest has been shown (Bard, 1952; Buell et al., 1971). This was also seen in surveys in Illinois old fields which showed a strong correlation between seed rain density for both wind and bird-dispersed tree species and forest edge (Burton, 1989). All these patterns taken together help to document differences in windows between species, between different areas in an old field and over successional time as animal abundance, site structural complexity and seed availability change.

C. PROCESSES DETERMINING TREE SEED SURVIVAL

1. Loss of Viability

Viability of tree seeds has not been tested in old field experiments directly, however emergence of trees in old field soils is very low (Gill & Marks, 1991; Livingston & Allessio, 1968; Oosting & Humphreys, 1940). In addition, extensive laboratory and greenhouse tests of seeds of old field tree species have shown that the period of viability lasts only a few weeks to a few months (Fowells, 1965; Schopmeyer, 1974). Rarely does viability extend to the next growing season (e.g. *Juniperus virginiana*) or for a few years (e.g. *Prunus sertronia*). In fact, emergence of some species (i.e. *Liriodendron tulipifera*; De Steven, 1991a) is limited by low seed viability. By far the most common pattern is fall dispersal of seeds, dormancy in winter and germination and establishment the following spring (Fowells, 1965; Schopmeyer, 1974). For each yearly seed crop windows may be restricted by the short period of viability exhibited by tree seeds in old fields.

2. *Fungus*

Evidence from experiments on eastern forest trees suggest that fungus attack is more common on tree seedlings than on tree seeds (Fowells, 1965; Schopmeyer, 1974). Even though a wide variety of fungi species attack tree seedlings, it results in little mortality in the eastern deciduous forest biome (Fowells, 1965). This suggests that attack by fungus and subsequent decay is a minor mechanism influencing old field tree seed survival and seedling mortality and growth.

3. *Predation*

Field experiments show that seed predation by small mammals may account for the largest losses of tree seed in an old field (Gill & Marks, 1991; Myster & Pickett, 1993) and potentially the greatest effect on seed invasion windows. In a 7-year old field at HMF, seed predation was greatest (96% – 99% loss) for *Acer rubrum*, *Quercus rubra* and *Cornus florida*, moderate (44% – 84%) for *Carya tomentosa* and *Fraxinus americana* and low (2%) for *Juniperus virginiana*. Reduction of predation by additions of *Quercus* litter and *Solidago* litter (Barnett, 1977; Myster & Pickett, 1993) implied spatial variation in seed predation because litter is spatially heterogeneous in HMF old fields (Facelli & Carson, 1991). *Carya tomentosa* seed predation was also reduced by increasing distance from the forest edge (Myster & Pickett, 1993). Spatial effects were demonstrated when seed predation was greater under woody patches compared to herbaceous patches (Myster & Pickett, 1993; Webb & Willson, 1985) and greater in herbaceous patches compared to open areas (Burton, 1989; Gill & Marks, 1991).

Temporal variation was implied when with increasing field age, from 7 to 17 years since abandonment, the order of decreasing seed preference changed from *Acer*, *Cornus*, *Carya*, *Quercus*, *Fraxinus* and *Juniperus* to *Quercus*, *Acer*, *Fraxinus* and *Carya*. A narrowing of invasion windows (Gross, 1980; Rankin & Pickett, 1989) was suggested when seed predators preferred larger seeds (De Steven, 1991a; Myster & Pickett, 1993) more common later in succession (Myster & Pickett, 1992a) and there was an increase in seed predation with age and structure of old fields (Myster & Pickett, 1993). De Steven (1991a) in North Carolina old fields showed interactions of predation with the environment when seed predation increased with spring rain.

D. TREE SEED GERMINATION

Tree seed germination is controlled by moisture and temperature conditions, with light characteristics also important (Schopmeyer, 1974). In old field experiments, germination of tree seeds and emergence of tree seedlings had greater sensitivity to variation in temperature than moisture, but this difference in sensitivity was reduced for larger seeds (Burton & Bazzaz, 1991). Consequently, species prevent emergence too early in the year when temperatures are low, and germination may increase with succession as temperature fluctuation is reduced (Bazzaz, 1979). An attempt to correlate these results with conditions under vegetation patches in the field showed that yearly differences in emergence overwhelmed any vegetation patch differences (Burton & Bazzaz, 1991). However, emergence of all species seemed negatively associated with leaf area and generally greater in open microsites, perhaps indicating some minimal light requirements (Burton & Bazzaz, 1991).

Because litter largely defines old field seed microsites, I investigated litter effects (both type and density) on germination in a greenhouse experiment near HMF. I found that *Quercus* spp. and *Solidago* spp. litter (the most common litter types in HMF old fields; Facelli & Carson, 1991) greatly reduced emergence of small-seeded bird-dispersed species *Juniperus virginiana* and *Cornus florida*. For mammal-dispersed species *Carya tomentosa* and *Quercus rubra*, all litter treatments reduced emergence except low density oak leaves which tended to promote emergence. *Quercus* emerged twice as often as *Carya*, *Juniperus*, and *Cornus* in control pots without litter. *Carya* emerged before other species and high density oak leaves significantly delayed opening of its cotyledons. For *Carya* and *Quercus* seedlings, litter reduced aboveground biomass but this was significant only for *Carya* (Myster, unpub.). My results suggest that litter may inhibit germination of early successional species and be critical for germination of later successional tree species (Schopmeyer, 1974) because it holds moisture for germination and reduces temperature and moisture variation (Beckwith, 1954; Coile, 1940; Korstian, 1927).

Illinois old field experiments showed species-specific variation in germination response to temperature and soil moisture. *Fraxinus americana* and *Morus rubra* had higher emergence at higher temperatures and moistures than other tree species and *Prunus serotina* had higher emergence at low temperatures. In addition, *Prunus* germination was negatively correlated with mean soil moisture and *Fraxinus* was negatively correlated with mean maximum temperatures (Burton, 1989, Burton & Bazzaz, 1991). In 10 year old North Carolina fields (De Steven, 1991a), experiments showed that germination of *Pinus taeda* was greater than hardwood species *Fraxinus americana*, *Liriodendron tulipifera*, *Acer rubrum*, *Liguidambar styaciflua* and *Ulmus alata*. Also, smaller seeded species germinated better than larger seeded species and herbaceous cover facilitated emergence of larger seeded species through maintenance of a moister microenvironment. Parallel greenhouse experiments generally supported these results except that germination was much greater in the greenhouse compared to the field (Myster, unpub.). Old field vegetation increases emergence compared to open areas especially for larger-seeded species (Gill & Marks, 1991; De Steven, 1991a) and drought can reduce emergence (De Steven, 1991a). Old field conditions needed for germination may be rare because rates of germination and emergence of seedlings in old fields are generally low (Burton & Bazzaz, 1991; De Steven, 1991a; Gill & Marks, 1991).

E. PROCESSES DETERMINING TREE SEEDLING GROWTH AND SURVIVAL

Many processes may potentially influence tree seedling growth and survival (Fig. 2). These include salt spray, radiation, acid rain, wildfires and flooding (Fowells, 1965). However, there is no observational or experimental evidence for these mechanisms in old fields and they will not be discussed.

1. Resource Limitation

Lack of sufficient moisture in the soil and occurrence of drought years in old fields seems to be an important kind of resource limitation (De Steven, 1991b). For example, losses of tree seedlings may be great in HMF marginal habitats during drought years (Davison, 1981). Observational evidence reveals that old field transition stages in Massachusetts (Spurr, 1956) and North Carolina (Billings, 1938; Crafton & Wells, 1934) vary greatly according to the moisture relationships of the soil. Also in North Carolina, lack of surface soil moisture is a primary cause of pine seedling mortality (McQuilkin, 1940) and oak establishment is controlled by water-holding capacity of the surface soil where litter is needed to hold moisture (Billings, 1938).

These results suggest that drought tolerance is an important trait for seedling success (Bazzaz, 1979; De Steven, 1991b). For example, *Juniperus virginiana* dominates many xeric sites (Bahari et al., 1985) and its establishment is helped by its drought resistance (Ormebee et al., 1976). Experimental results show that drought years magnify reduction of tree seedling survival in vegetation patches (De Steven, 1991b) and at HMF drought leads to tree seedling mortality in old fields (Myster & McCarthy, 1989). Drought can also change competitive relationships as when *Quercus* spp. seedlings have a competitive growth advantage over *Cornus florida* and *Acer saccharum* seedlings (Bahari et al., 1985).

Invasion of old fields by trees is also affected by availability of nitrogen or other soil nutrients which may increase through succession (Tilman, 1988). This is implied when trees bring up nutrients from deeper soil layers and accelerate succession locally (Whitford & Whitford, 1978). It is also consistent with a pattern of *Pinus taeda* on the most nutrient rich sites in North Carolina, *Pinus virginiana* on the poorest, and *Pinus echinata* on intermediate sites (Toumey & Korstian, 1937). This group of factors needs further experimentation in old fields.

2. Frost-heaving

Frost-heaving, where the freeze-thaw cycles of winter pull seedlings out of the ground, may be a cause of seedling root damage, growth modification and mortality (Buell et al., 1971). Frost-heaving has temporal variation because it is more common early in succession when litter, which may have an indirect effect of reducing frost-heaving, is not present (Buell et al., 1971). Herbs also may have an indirect effect of reducing frost heaving (Gill & Marks, 1991). Consequently, frost-heaving has spatial variation because oak litter is more common next to the forest edge (Facelli & Carson, 1991) and vegetation is spatially heterogenous. *Acer* spp. are among the most sensitive species to frost-heaving (Buell et al., 1971; Burton, 1989) but, no losses of *Carya tomentosa* seedlings due to frost-heaving were seen in a two-year seedling survival experiment done in a 7-year old field at HMF (Myster & McCarthy, 1989).

3. Physical Damage

Physical damage to seedlings that may lead to mortality include snow and wind damage (Fowells, 1965), trampling by animals and damage from falling trees, branches, twigs and litter (McCarthy & Facelli, 1990). In an experiment at HMF, losses of artificial tree seedlings in 5 year old fields were due mainly to snow and wind damage. Spatial variation of physical damage was implied when artificial tree seedlings in sparse cover suffered greater mortality than in open areas (McCarthy & Facelli, 1990).

4. Competition

Establishment windows can be reduced or closed by competition (Rankin & Pickett, 1989) which is suggested by the inhibition of trees by dense herbaceous vegetation (De Steven, 1991b; Egler, 1954; Harper, 1977; Werner & Harbeck, 1982) and by increases in woody growth after disturbance of the herbaceous vegetation (Armesto & Pickett, 1985). Two of the major resources for which plants compete in old fields are moisture and light (Bazzaz, 1968; Buell et al., 1971; Crafton & Wells, 1934) and plants may choose during succession between allocation strategies that favor shade intolerance or tolerance to root competition (Beckwith, 1954; Tilman, 1988). Experiments show old field plants can inhibit tree seedlings by competing for water (van Allen, 1970; Zulter et al., 1986). Consequently, an efficient root system is important for the establishment of trees (Duncan, 1935; Eissenstat & Mitchell, 1983), and many tree species have deep seedling roots which aid establishment by passing through the zone of greatest competition (Billings, 1938; Coile, 1940).

Competition for light is implicated as affecting tree seedling growth in old fields (Bazzaz, 1979) by observations that later successional trees have greater shade tolerance than earlier species (Beckwith, 1954; Billings, 1938; Finegan, 1984; Parrish & Bazzaz, 1982), and there are lower densities of tree seedlings in areas covered with tall herbaceous vegetation (Pound & Egler, 1953; Werner & Harbeck, 1982). For example, *Juniperus* may be excluded from mature forests because it is shade-intolerant (Bard, 1952; Bazzaz, 1979; Ormsbee et al., 1976). In addition, there is a close relationship between old field sequences of species replacement and shade tolerances. For example in Michigan, the sequence of increasing tolerance with time includes *Fagus* spp. and *Acer* spp. followed by *Quercus* spp. and *Carya* spp. (Beckwith, 1954). In North Carolina, the sequence includes *Oxydendron arboreum, Ulmus alata, Cornus florida, Pinus taeda* and *Pinus echinata* followed by *Celtis tenuifolia, Liriodendron tulipifera, Nyssa sylvatica* and *Quercus stellata* and finally *Fagus americana, Carya glabra, C. tomentosa, Quercus rubra* in North Carolina (Billings, 1938). Oaks and hickories may become dominant in North Carolina because pine cannot perpetuate itself under its own shade (Billings, 1938).

Experimental evidence of competition has been seen in tree seedling plantings in different vegetation patches. In Illinois old fields, evidence of tree seedling competition is species and patch-type dependent. The vegetation patch type of lowest competition varied between species and age of seedling. *Acer saccharem* was the most competition-tolerant species and *Prunus serotina* the least competition-tolerant. First-year *Setaria* dominated fields were the most conducive to tree seedling establishment and *Prunus* spp. canopies were the most inhibitory (Burton, 1989). However, at HMF diffuse competition between tree seedlings and old field plants did not reduce growth or survival of seedlings after they were 25 cm in height (Myster & McCarthy, 1989), and in New York old fields competition with herbs decreased tree seedling growth but not survival (Gill & Marks, 1991). In North Carolina, old field vegetation reduced survival but competitive reductions were small for all species except *Liriodendron* and height growth was strongly reduced by vegetation for all tree species except *Pinus* (De Steven, 1991b). These mixed results suggest that competition is important but that other processes may be more critical in controlling seedling survival and growth.

Plants may have allelopathic effects on tree seedlings (Rice, 1974). Experiments have shown that residue from asters and goldenrods inhibit germination and growth of *Acer* spp. and *Prunus serotina* seedlings (Fisher et al., 1978). Observations support the hypothesis that *Sassafras albidum* helps maintain itself by allelopathy (Gant & Clebsch, 1975) which suppresses other old field plant species. In addition, allelopathic or competitive interactions were suggested in BSS old fields when *Juniperus virginiana* had a repeated negative association with *Solidago juncea* (Myster & Pickett, 1992b).

Old field plant species may also facilitate tree establishment. Observational evidence suggests that shrubs create mesic conditions for tree germination (Duncan, 1935) and that trees bring up nutrients from deeper soil layers and increase tree establishment locally (Whitford & Whitford, 1978). Also, the increase in tree density under *Rhus typhina* may be the result of a reduction of competition (Duncan, 1935) and *Rhus* spp. may indirectly create safe sites for tree seedlings by reducing herbaceous vegetation and increasing dispersal of tree seeds by birds (Werner & Harbeck, 1982). At HMF, *Rhus radicans* is positively associated with *Juniperus virginiana* (Myster & Pickett, 1922b), *Juniperus* opens up space necessary for oak tree establishment (Bard, 1952), trees facilitate tree establishment by acting as recruitment foci for bird-dispersed tree species (McDonnell & Stiles, 1983), and oak litter may indirectly enhance tree seedling survival by inhibiting growth of competing herbs (Facelli & Pickett, 1989, 1991).

5. *Predation/Herbivory*

Predation and herbivory by mammals may narrow or close windows extensively (Rankin & Pickett, 1989) because experiments have found predation on old field tree seedlings to be intense (Gill & Marks, 1991; Myster & McCarthy, 1989). In HMF old fields, *Carya tomentosa* seedlings suffered great mortality (Myster & McCarthy, 1989) and tree species differed in palatability to herbivores with *Quercus alba* and *Acer rubrum* > *Fraxinus americana* and *Cornus florida* > *Juniperus virginiana* (Meadows, 1988). Field experiments have shown spatial variation in effect of predation when seedlings planted away from the forest edge suffered significantly less predation than those closer to the forest (Myster & McCarthy, 1989) and when predation was greater in herbaceous patches compared to open areas (Gill & Marks, 1991). Additional spatial variation of predation was implied at HMF when survival of *Acer rubrum*, *Quercus rubra*, and *Cornus florida* was directly proportional to *Solidago* spp. cover, palatable species *Quercus* spp. and *Cornus florida* showed greater predation reduction under cover than less palatable species (Meadows et al., 1989), and spatially heterogeneous oak litter (Facelli & Carson, 1991) indirectly increased predation by increasing abundance of arthropods (Facelli & Pickett, 1991).

Temporal variation was shown when predation on *Acer rubrum* seedlings increased with successional time which may narrow its invasion window (Rankin, 1981). Seedling mortality is probably due to mammalian predation because insect herbivory was not reported to kill any seedling or significantly alter any seedlings growth in field experiments (Myster & McCarthy, 1989). It is worth noting that some windows reopen after being closed because seedlings (e.g. *Carya tomentosa*) may resprout after complete browsing (Buell et al., 1971, Myster & McCarthy, 1989).

V. Synthesis

Answering the major review questions of pattern and process of tree invasion and establishment must involve reference to multiple processes (De Steven, 1991a,b; Finegen, 1984; Myster & McCarthy, 1989; Pickett et al., 1987). To understand the relative roles of these processes, presented is a summary of the variation in seed and seedling mortality among studies with their spatial/temporal variation. Seed losses to fungus are low but losses to predation can range up to 75%–100% (De Steven, 1991a; Gill & Marks, 1991; Myster & Pickett, 1993). When germination does not occur, losses of seed viability are large because emergence rates are low in old fields (6%–12%, Burton & Bazzaz, 1991; De Steven, 1991a; Gill & Marks, 1991).

For seedlings in HMF and New York old fields, competition with herbs did not reduce survival (Gill & Marks, 1991; Myster & McCarthy, 1989), but in Illinois, between 0% and 30% of seedlings were lost depending on patch type (Burton, 1989), and in North Carolina there was a 30%–90% loss in vegetation patches (De Steven, 1991b). The greatest losses of seedlings came from predation (34%–100%, De Steven, 1991b; Gill & Marks, 1991; Myster & McCarthy, 1989). Frost heaving killed between 0% and 23% of seedlings in old field experiments (Gill & Marks, 1991; Myster & McCarthy, 1989). Mortality of seedlings from physical damage was between 5%–15% in experiments using artificial wooden seedlings (McCarthy & Facelli, 1989) and losses due to drought and insect herbivory were from 0%–2% (Myster & McCarthy, 1989).

Combining these results with an analysis of spatial establishment pattern suggests critical roles for dispersal (Myster & Pickett, 1992a), conditions needed for germination (Burton & Bazzaz, 1991; Myster, unpub.) and seed and seedling predation (Gill & Marks, 1991; Myster & McCarthy, 1989; Myster & Pickett, 1993) in determining tree invasion and establishment in old fields. Many of these same processes are also thought to be critical in tropical forest regeneration (Schupp, 1990). The remaining processes that affect tree seeds and seedlings (Fig. 2) may play important roles in modifying general patterns of tree invasion and establishment determined by the more critical processes. The net effect of all processes on tree establishment addresses the question of safe sites (Harper, 1977). For example, processes may combine to reduce tree establishment under herbs compared to openings (Gill & Marks, 1991) and therefore the rapid decline in openings through succession may close windows quickly and help explain the fairly even age structure of populations of early woody invaders (Gill & Marks, 1991; Rankin & Pickett, 1989). Because some processes increase while others decrease establishment in the same patch type, a tentative conclusion is that the net effect of seed and seedling processes is to produce very low probabilities of tree establishment (Gill & Marks, 1991; Myster, unpub.) which may help explain the slow rate of tree invasion and establishment (Bazzaz, 1968; Buell et al., 1971; Tilman, 1988). For a tree to grow in an old field, its seed must first disperse and germinate and then avoid the twin hurdles of seed and seedling predation. We have seen that these processes greatly affect invasion and establishment opportunities by opening or closing windows. To reflect the dynamic nature of these windows I have reviewed the spatial variation, the temporal variation and the difference among species in effect of these processes. *Juniperus*, a dominant and characteristic old field tree species (Bard, 1952; Bazzaz, 1968), illustrates how the critical processes of fast and extensive regeneration combine to affect rate and pattern of tree succession. The seed of *Juniperus* is readily dispersed (McDonnell & Stiles, 1983), suffers almost no seed loss to predators (Holthuijzen & Sharik, 1985; Myster & Pickett, 1993) and its seedlings are little browzed (Meadows et al., 1989).

It is useful to explore the interaction of pattern and process in tree invasion and establishment dynamics (Huston & DeAnglis, 1987; Watt, 1947) for a more realistic view of forest regeneration. By pattern I mean the spatial and temporal pattern of tree invasion and establishment in old fields and by process I mean the total array of processes influencing and being influenced by that pattern. In old fields, processes such as dispersal and seed and seedling predation are influenced by the presence, density and spatial arrangement of trees and other plants (Burton, 1989). Conversely, these processes define new tree establishment patterns by affecting probabilities of tree establishment in different areas in an old field. For example, wind-dispersed seed is affected by the change in wind patterns around trees (Carol Augsburger, pers. comm.), the density of bird-dispersed seeds is greater under trees than in open old fields (Burton, 1989; McDonnell & Stiles, 1983) and the density of mammal-dispersed seeds may be greater under patches of woody cover used by small dispersing mammals for protection from their predators (Hanson et al., 1969). Conversely, dispersal influences new establishment patterns as seen by the exponential decline in density from the forest edge and clumping of bird-dispersed species (Myster & Pickett, 1992a). Seed predation is also affected by tree spatial arrangement when predators feed preferentially in woody patches or in older, more woody and spatially complex old fields (Burton & Bazzaz, 1991; Myster & Pickett, 1993; Newman et al., 1988). In addition, seed predation is reduced by *Quercus* spp. litter patches that are greatest next to the forest trees (Myster & Pickett, 1993). Seedling predation is also affected by spatial arrangement of trees because it is reduced in herbaceous patches compared to woody patches (Hanson et al., 1969) and herbivory decreases with increasing distance from forest edge (Myster & McCarthy, 1989). All relevant studies reviewed conclude that spatial variation in predation on seeds and seedlings can affect the spatial arrangement of future tree establishment by changing invasion windows.

VI. Concluding Remarks

This review has organized information concerning tree invasion and establishment in the eastern United States old fields and pinpointed areas where documentation of spatial, temporal and species variation in processes that determine survival and growth of tree seeds and seedlings in old fields is lacking. Although complete documentation of the variation in critical processes and their interaction with other processes and the environment is a future goal, experiments here revealed important variation and this information allows a more complete understanding of the causes of the old field tree establishment patterns. Further field experiments are needed over a wider range of fields and especially over longer periods of time. It must also be remembered that many of my conclusions concerning processes may be biased because they are based mainly on old field experiments in the northeastern United States. For example in the southeastern United States, old field tree succession may be more rapid and fields more prone to spring drought (De Steven, 1991a,b). Further detailed experimentation is essential due to the species-specific nature of biotic resistance to invasion (Burton, 1989). Another goal of future experiments besides this documentation of variation, must be the elucidation of the effect of processes important at the invasion stage on establishment (sensu Louda, 1982) and consequently the net effect of mechanisms on establishment. Future research at HMF will combine additional analysis of the BSS study data with field experiments. The BSS data set will be used in spatial statistical techniques such as spatial autocorrelation, trend surface analysis and kriging (Matheron, 1963) to discover patch configuration and topology of invasion. The ultimate goal of all research into tree invasion and establishment in old fields and a major motivation for this review will be the development of a mathematical model of tree establishment in old fields.

VII. Acknowledgements

I would like to thank Dr. Helen Buell for her help in setting up the BSS and her continuing help in sampling. I would also like to thank Drs. U. Vedagiri, D. De Steven and P. Burton for commenting on earlier versions of the manuscript and Dr. D. Schaefer and Ms. E. Melendez of the Terrestrial Ecology Division, University of Puerto Rico for help in the Spanish translation of the abstract. I also thank members of my doctoral committee, Drs. Mark McDonnell, Steven Handel, Peter Morin and my advisor Steward Pickett. Results from my research referred to in this review was supported by Sigma Xi grants-in-aid of research, HMF summer fellowships and NSF doctoral dissertation improvement grant BSR–8901209. Additional support was provided by the Mary Flagler Cary Charitable Trust which is a contribution to the program of the Institute of Ecosystem Studies, New York Botanical Garden.

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