Population-Level Processes: Seed and Seedbed Ecology

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Abstract

Seeds play an important part in the vegetation of disturbed areas through germination from natural or artificial seedbanks, natural seed dispersal, or artificial seeding. The density and species composition of the plant communities thatt colonize disturbed areas depend on the inherent physiological systems of the seeds and potential of the seedbed to support germination. Inherent physiology can be modified by pretreatment such as seed scarification of species with indurate seed coats. The potential of the seedbed can be modified by seedbed preparation and seeding techniques.

Introduction

The most economical method of establishing vegetation cover on an area that has been drastically disturbed is usually through planting seeds, seed germination, and subsequent seedling establishment. This process can be the result of natural succession, germination from conserved topsoil that was reapplied to a disturbed site, or through artificial planting. The success of the revegetation process depends on the inherent potential of the physiological systems of the seeds that are naturally dispersed across the site or artificially placed in the seedbed, and equally important, the potential of the seedbed to support germination.

The concept of the seedbed having varying potentials to support germination may seem odd, but it is the basis for most farming practices designed to assure adequate stands. Tillage practices such as plowing may be initially done for seed control, but subsequent operations such as harrowing and cultipacking are primarily designed to make certain seeds are planted or drilled at the proper depth, covered with soil, and adequate contact between soil particles and the seed coat is established. The interesting aspect of seedbed potential is how we can manipulate the beds to make them a selective filter to govern the species composition of post-disturbance communities.

It is perhaps easier to contemplate that seeds vary in their potential to germinate in a specific seedbed. We can manipulate such differences by selecting specific cultivars to be included in revegetation mixtures. It is also possible to change the germination characteristics of seeds by physical, chemical, or physiological manipulations done before the seeds are planted.

The purpose of this synthesis paper is to draw together various aspects of seed and seedbed ecology that have practical applications to the revegetation of disturbed environments.

Seedbanks

Seedbanks refer to the number of viable seeds per volume of surface soils. In agronomic soils, the seeds in the seedbank may be distributed through the tillage depth. In wildland situations where tillage is not practiced the bulk of viable seeds may be located in the litter and duff, on or very close to the soil surface. Fine textured soils that crack will have the cracks filled with seeds. There is always some seed burial by small mammals and insects. In temperate desert environments seed collection and caching in scatter hoards by Heteromyid rodents is a very significant component of seedbank enrichment (Longland 1987). At the same time, predation of seeds in seedbanks may be a major source of seed loss (Louda 1989). Microscopic seeds may find their way to considerable depths in the soil through soil pores or by ingestion by soil arthropods (Major and Pyott 1966).

It is very tempting to generate flow diagrams to illustrate the processes involved in seedbanks. An often cited example is that of Harper (1977) or the more recent effort by Simpson and others (1989). I admit to attempting such diagrams (Young and others 1981; McAdoo and others 1983; Young and Evans 1985). These flow diagrams probably serve a purpose as conceptual models, but unfortunately, they also seem to become absolute. Numerous young scientists are in the process of quantifying and assigning probability levels to the various aspects of specific models for seedbanks (e.g., William Longland and *Oryzopsis hymenoides,* unpublished research ARS-USDA, Reno, NV). Diagrams for seedbank functions are available in the literature for reference by readers, but remember they are probably incomplete generalizations that should not curb experimentation.

If you are going to manage and manipulate soil seedbanks as a source of seeds for revegetation of disturbed areas, you are concerned with a rather thin, organically rich layer near the soil surface. Much thicker layers of the soil profile may be stripped and stockpiled for topsoiling disturbed areas, but the primary purpose of such operations is to provide a medium for plant growth.

Seedbank transfer may be incidental to such manipulations. Seedbanks reflect the heterogeneity of the site where they were produced. It may be profitable to selectively collect topsoil from specific sites that have seedbanks rich in seeds of desired species. In degraded big sagebrush *(Artemisia tridentata)* communities, virtually all viable seeds are located beneath the shrub canopies, and the interspace between shrubs is devoid of seeds (Eckert et al. 1989)

Nature of Seeds in Seedbanks

Depending on the season of the year, the seedbank may contain seeds of the current year's seed rain or may be composed entirely of seeds carried over from previous years' production. When dealing with seedbanks as a means of revegetating disturbed areas, one must remember that you can get weeds as well as desirable species. In fact, many weed species have seeds that are adapted to prolonged burial in soil seedbanks and they are triggered to germinate by disturbance. For seeds to remain in the seedbank for long periods, they must either be physiologically dormant or induced to dormancy by being in a position where they cannot germinate.

In a synthesis chapter in the most recent review of seedbanks, Parker et al. (1989) suggested that soil seedbanks are more likely to resemble early successional than late successional vegetation. They cite many examples, but as with any generalizations there are exceptions. In the annual ranges of California where the vegetation must be renewed annually from the seedbank, the seeds of the dominant grasses dominate the seedbank (Young et al. 1981).

Seeds may be physiologically dormant in the seedbank because of hard seedcoats that inhibit moisture or gas diffusion to or from the embryo because of light requirements for germination, or because of insufficient concentrations of chemicals that promote germination (see Baskin and Baskin 1989). In very wet muck soils, lack of oxygen may inhibit germination. When you store soils for later use in topsoil applications it is important to realize that the conditions that promote dormancy may be changed and the dormant seeds may germinate and die before the soil is spread on the disturbed area to be vegetated. Remember that the biologically most active zone of the soil profile, as far as seedbanks are concerned, is the surface, with associated litter and duff. If this organic matter is placed in a position where active decomposition is enhanced, the environment for the seedbank will be dramatically changed. I am not experienced with storing topsoil for future plant establishment of plant communities from seedbanks, but piled or piled and covered topsoil may offer better storage of seeds than spread layers of soil.

Johnson and West (1989) obtained samples from topsoil stockpiles of three different ages on a coal strip mine in order to determine the infuence of time and depth of burial on germination and species composition. The number of viable seeds increased with increased storage time. Differences in predisturbance vegetation and soil depth are likely factors determining the seeds in stockpiled topsoil.

Storage Life of Seedbanks

Some seeds have very short half-lives in the soil and therefore are largely absent from seedbanks. Big sagebrush is an excellent example of this type of seed. In western Nevada, seed of big sagebrush is mature in late November or early December, and by the following June, seeds are largely lost from the seedbank (Table 1) (Young and Evans 1989). Establishing big sagebrush has been a major problem on restored strip mine areas in the American West.

Table 1.—Emergence of seedlings of big sagebrush (*Artemisia tridentata*) from soil samples collected periodically throughout the year at 5 locations; based on means of seedling emergence data collected from 1983 through 1986 (Young and Evans 1989)

		Big sagebrush seedling emergence, sample collection dates							
Location	Subspecies	Dec. 1	Jan. 15	March 1	April 15	June 1	July 15	Sept. 1	Oct. 15
		(no./0.01m²)							
Granite Peak	Mountain	0	560 ab	300 b	30 b	0	0	0	0
Churchill Canyon #5	Mountain	0	680 a	560 a	180 a	0	0	0	0
Churchill Canyon #1	Basin	0	10 c	0 c	0 b	0	0	0	0
Churchill Canyon #4	Basin	0	120 c	30 c	0 b	0	0	0	0
Medell Flat	Basin	0	480 b	510 a	190 a	0	0	0	0

[a]Means within rows followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test. No letters indicate no significant differences.

The concept of donor seedbanks has been proposed for restoring wetlands (van de Valk and Pederson 1989). Many wetland species are very difficult to establish from direct seeding (e.g., George and Young 1977; Cluff and Roundy 1988). Muck from an established wetland is excavated and dumped in the new area. Careful water management is required for this system to be successful.

Ecophysiology of Seeds

A major problem in environmental restoration is that plant communities reproduce in the minds of ecologists and plants reproduce from seeds. Unfortunately seeds do not always cooperate with the efforts of man. For many agronomic species, germination problems have been overcome through selection unless absent some basic physiological block. The seeds of many wildland species have germination systems that have been naturally selected to fit specific environmental situations where they are adapted. If these species are adapted to colonizing highly disturbed areas, there may be no problems, but if the desired species are adapted to some advance successional stage in a woodland, there may be considerable difficulties in getting the species established.

There are two basic self-evident truths in seed ecophysiology: 1) the seed of most species germinate without pretreatment, and 2) the physiological requirements conditioning dormant seeds can often be overcome by more than one method. At maturity, most seeds of plants of the temperate zone dry to about 8 to 10% moisture content and are kept in a dormant state by desiccation until they are allowed to imbibe moisture. This is a very simple system. There are recalcitrant seeds that cannot be dried to low levels of seed moisture content. Members of the genus *Araucaria* usually have recalcitrant seeds. The seeds of numerous species of tropical forests have recalcitrant seeds that have very short half-lives in storage.

The fact that dormant seeds can often be made to germinate by more than one and often dramatically contrasting methods is attributed to the cyclic nature of the biochemical processes that control the physiology of seeds (Roberts 1973). One of the many examples of this is the seeds of the common mullein *(Verbascum thapsus)*. The seeds of common mullein are initially dormant, but the dormancy is easily overcome by exposing imbibed seeds to red light. The seeds can be made to germinate in the dark if incubated at widely fluctuating incubation temperatures (Semenza et al. 1978). There are hundreds of other examples of similar phenomena in seed germination that may lead the casual observer, who is only interested in establishing a vegetation cover on disturbed lands, to suggest that seed physiology is a perfect example of chaos. There are repeated patterns in the entire germination process that bring relative understanding to chaos.

Hard Seed Coats

Indurate seed coats that interfere with moisture imbibition and sometimes the movement of gasses to embryos are a major source of seed dormancy. Members of the legume family often produce seeds with hard seed coats. The high-protein seeds of legumes are the target of numerous seed predators.

In many parts of the world, seed beetles (Bruchidae) infest seeds of the *Acacia* species (Halevy 1974). The insect larvae will render the seeds nonviable if the insect is allowed to complete its life cycle. Large herbivores are attracted to maturing legumes of *Acacia* species in East Africa and they consume large quantities of the fruit. Digestive fluids in the rumen selectively kill the larvae of the bruchid beetle without reducing the viability of the seeds (Lamprey et al. 1974). Digestive juices may also influence the seed coats of the seeds. Domestic livestock consume significant quantities of fallen *Acacia tortilis* seed pods in arid pastoral ecosystems of northwest Kenya (Coughenour and Detling 1986). These seeds are subsequently defecated in corrals where dense populations of this species of *Acacia* arise. Periodic wildfires that burn through *Acacia* stands also selectively influence the bruchid beetle. The larvae of the beetle is killed by lower temperatures than the minimal lethal temperature for seed viability. Again the fire is a double action factor in that it not only kills the insect larvae but also may influence subsequent germination by altering the seed coat. The net effect is that legumes often develop large seedbanks, even in subtropical environments with rapid decomposition.

Using leguminous seedbanks for revegetation of disturbed areas is dependent on triggering the hard seed coats to become permeable. There is no good working hypothesis of how seeds with hard seed coats become permeable in seedbanks. Microbial decomposition, cracking from freezing or diurnal temperature fluctuations, and heat from wildfires have been suggested as natural means of breaking down hard seed coats. The greatest experimental evidence exists for the influence of fires on germination of hard seeded species (e.g., Gratkowski 1962).

Planting seeds with hard seed coats requires several considerations. If a portion of the seeds in a given seed lot has hard seed coats, prolonged germination over more than one season is assured, which may be an advantage in some situations. If the majority of the seeds in a given lot are dormant because of hard seed coats, pretreatment in the form of scarification is required.

Scarification can be accomplished with mechanical, acid, or thermal shock treatments. Virtually all scarification treatments, even when applied correctly, reduce total seed viability and potentially can drastically reduce seed viability. The basic problem with scarification treatments is that the amount of scarification that is required varies among lots of

the same species, making preliminary testing of each seedlot advisable.

In developing countries with large seeds of valuable tree species, scarification is often done by hand with a knife or file. Usually it is not necessary to remove the entire seed coat, only to break a small area. Many seeds with hard seed coats have very specific, often small structures in the seed scar area that control moisture imbibition. Mechanical scarification involves rubbing the seeds against an abrasive surface so the seed coat is broken. In some species mechanical scarification results in damage to exposed embryos and loss of viability. The most common treatment is acid scarification with concentrated sulfuric acid. Before you undertake acid seed scarification consider: 1) sulfuric acid is dangerous to handle, 2) prolonged treatment will kill the seeds, 3) acid scarified seeds are often susceptible to soil borne pathogens, and 4) you are creating a toxic waste, used acid, that requires disposal. The heat and chemical reactions associated with acid scarification have ramifications far beyond mere removal of seed coats (e.g., McDonald and Khan 1983). If you have no choice but to proceed with acid scarification, review the classic paper on the subject by Heit (1967).

Hot water treatments are much simpler than mechanical or acid scarification, but unfortunately they are not effective on all species. Bring a volume of water four times the volume of the seeds being treated to a boil and drop in the seeds. Remove the container from the heat and allow the seeds to stand in the cooling water overnight.

When dealing with seeds of species that potentially have hard seed coats, an old nurseryman's trick is to harvest the seeds early, before they are fully dry, and plant the seeds at once, being careful to never allow them to dry. This is effective for a surprising number of species (Young and Young 1990).

Afterripening Versus Prechilling Requirements

This is an often misunderstood portion of seed ecophysiology. I define afterripening requirements as dormancy that is overcome by passage of time after harvest, independent of storage conditions. In contrast, prechilling requirements are a form of dormancy that is overcome by a period of incubation, in an imbibed condition, at temperatures too low to permit germination.

Seeds of Russian thistle *(Salsola australis* R. Br.) provide a good example of afterripening requirements (Fig. 1). In this case, the afterripening requirement is related to incubation temperature, but not to storage temperature (Young and Evans 1972). Environmentally sensitive dormant seeds include seeds with warm-moist pretreatment requirements, or temperature specific incubation requirements that decrease over time. I must warn you that no one else follows these definitions, so you are faced with a bewildering array of dormancy conditions collectively termed afterripening requirements.

Afterripening that is immune to external stimuli requires only patience and it goes away. If you have a revegetation contract that requires plants to be emerged by a certain date and only fresh seed is available, you are in a difficult position. The seeds of some grass species can have the duration of afterripening requirements reduced by heating in forced draft ovens in accelerated afterripening treatments (Taylorson and Brown 1977). Note that by my definition this would not be termed afterripening because the dormancy can be broken by an external stimuli. It has been suggested that my definition is invalid because all cases of apparent afterripening requirements can be manipulated by external stimuli. We just have not discovered the correct treatments.

For species native to temperate regions the most frequent form of dormancy can be overcome by moist prechilling (Fig. 2). Some seed physiologists have even suggested that seeds of certain tropical species have enhanced germination following prechilling, even though the species are native to environments where it never gets cold. If you are not familiar with the term prechilling it is because it recently has come into general use to replace stratificiation. Despite its rich historical roots in northern European forestry, stratification is being discarded for the self descriptive prechilling.

The general rationale for prechilling requirements is that seeds mature in late summer or fall and are dispersed to the seedbed where they ideally lie under snow cover until the spring. The interface between snow and soil usually provides an ideal prechilling environment of near 0°C. Unless you are going to artifically pretreat seeds that have prechilling requirements you are forced to use fall planting. For species such as bitterbrush *(Purshia tridentata),* where the seeds are subject to predation, fall seeding may lead to large losses of seeds to rodents. The problem with prechilling seeds artificially is that the seeds cannot be dried after the prechilling requirement is satisfied so you are faced with mechanically handling a wet seed. This can be done by gel seeding (Booth 1985).

Warm-Moist Pretreatment

A considerable number of species, especially those native to subhumid and humid regions, produce seeds that have dormancy-breaking requirements which include a period of incubation under warm-moist conditions. For want of better terminology these are still referred to as warm stratification requirements. Without pretreatment of seeds of these species, they have to be planted very early in the fall or emergence will be delayed until a second year after planting. Several species of woody plants native to eastern North America have prechilling requirements that must be preceded by warm-moist incubation. Termed double dormant species, these species require 2 years after natural seed fall to emerge.

Practical revegetation attempts, including these double dormant seeds in mixtures, can lead to problems if

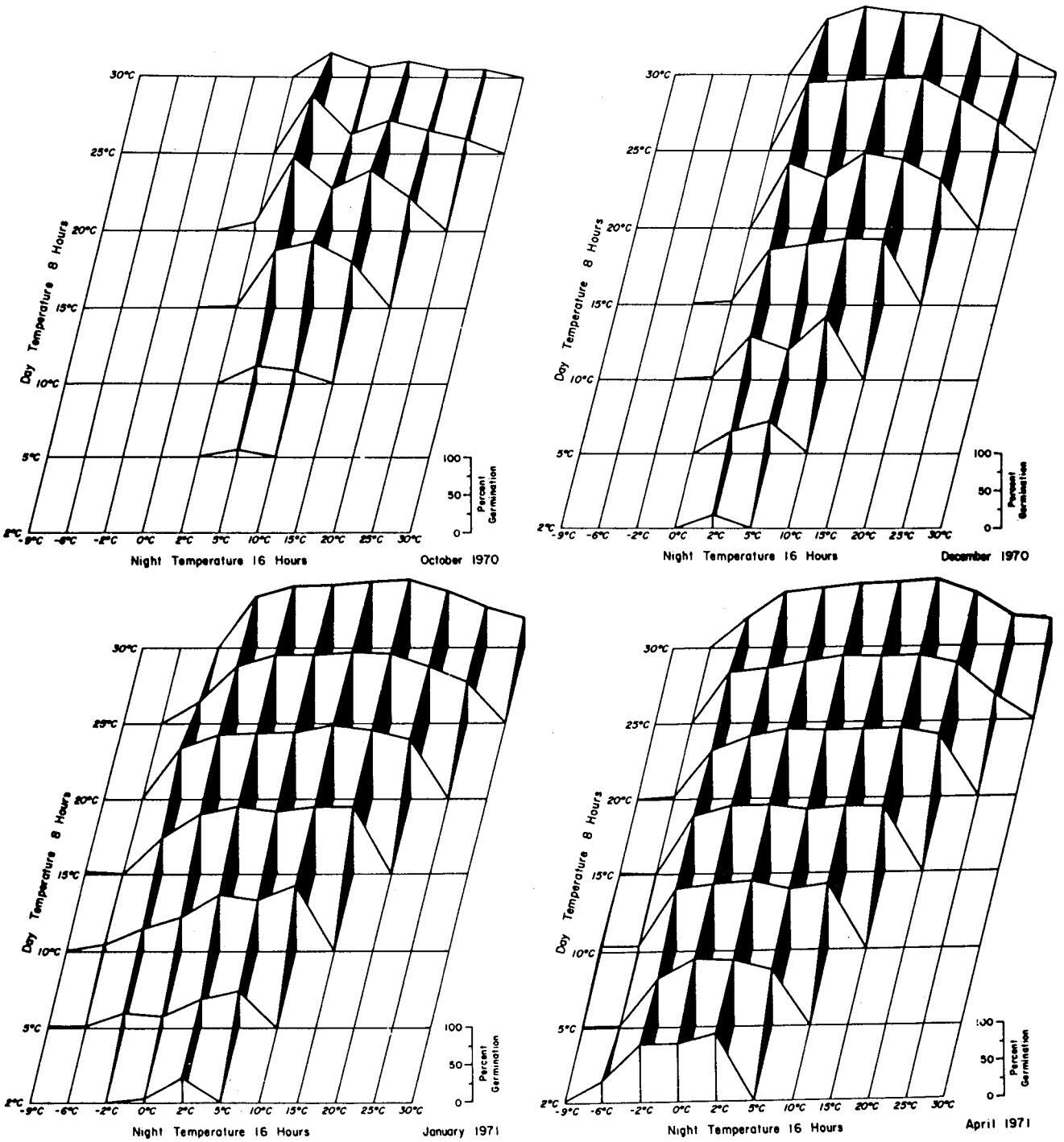

Figure 1.—Germination of *Salsola australis* (*S. iberica*) seeds in relation to temperature related afterripening requirements (Young and Evans 1972).

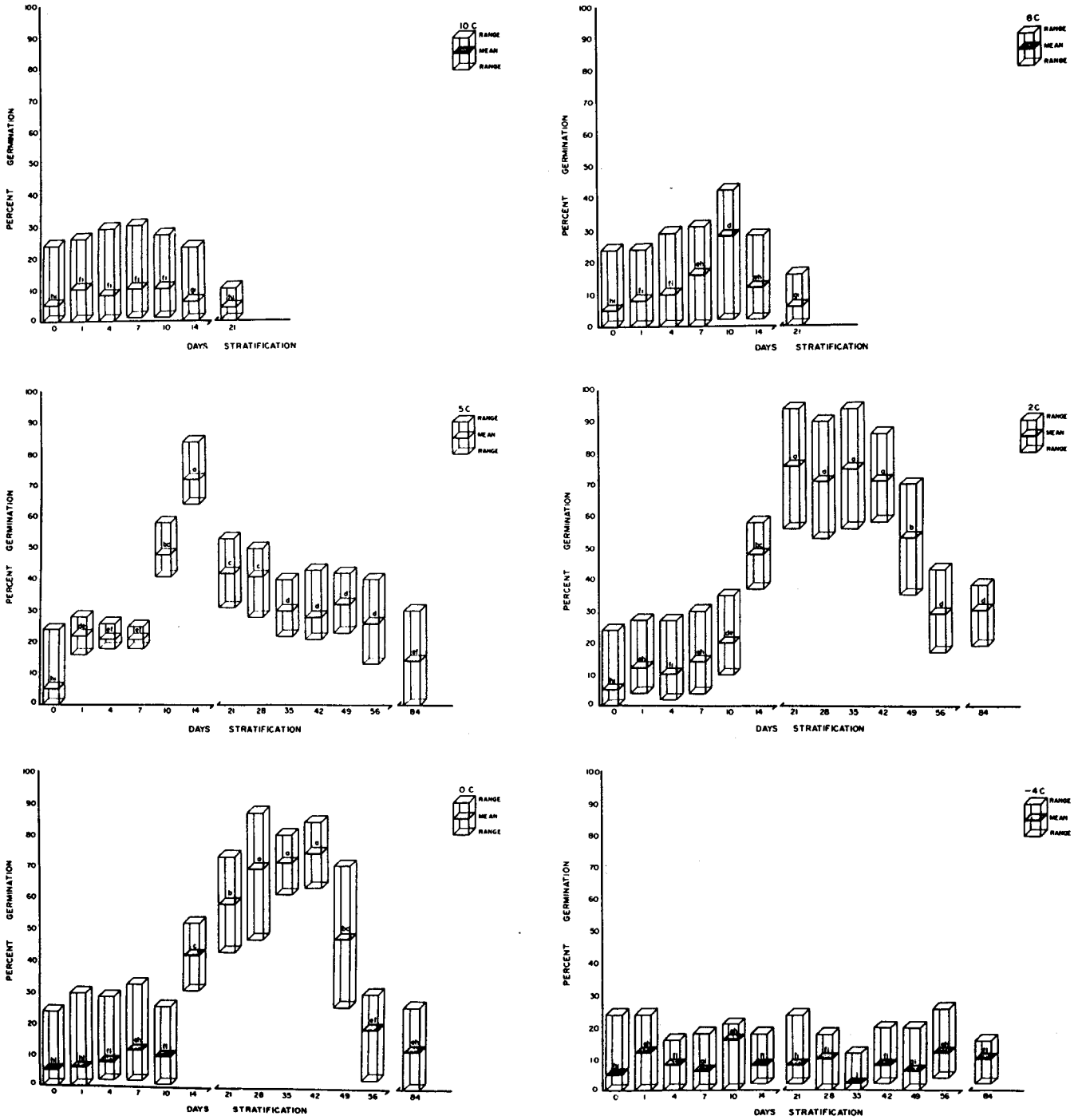

Figure 2.—Germination (mean and range) of six lots of bitterbrush seed (*Purshia tridentata*) incubated at 15°C after stratification at temperature of -4, 0, 2, 5, 8, and 10°C, from 0 through 84 days. No germination was observed in seed stratified longer than 21 days at 8 and 10°C. Means (bars) with the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test (Young and Evans 1976).

herbaceous species are successfully established the first season after seeding. By the time the double dormant species germinate, there may be no environmental potential available for them for establishment. It may be more biologically and cost effective to transplant seedlings of nursery grown stock of double dormant species than to attempt to grow such species from seed in a mixture.

Light

Seed germination can be affected by the quality of light, duration of light (photo period), and, rarely, by the presence of light. One of the most spectacular means of inducing dormant seeds to germinate is by exposing imbibed seeds to red light if they are sensitive to phytochrome (e.g., Borthwick et al. 1952). The reversible phytochrome reaction is a very important part of seed ecophysiology. Not all seeds are sensitive to light. Many seeds are neutral to light in their germination response. In 30 years of research in this field I have experienced one species of *Galium* where seed germination was inhibited by light.

It seems to be a general consensus that little light is transmitted through even thin layers of soil. Studies by Kasperbauer and Hunt (1988) indicated that less than 0.005% of the incident light penetrated 4 mm in dark colored soils or 10 mm of gray-white soil. Light requiring seeds of tobacco *(Nicotiana tobacum* L.) used to bioassay for light had 99% germination on the soil surface and no germination when buried 4 mm in the soil. This means that light-sensitive seeds must be exposed on the surface of the seedbed if they are going to have germination stimulated by light. Exposure on the surface of seedbeds can place seeds in very unfavorable moisture conditions. The seed must take up moisture from partial contact with the particles that compose the seedbed while at the same time lose moisture to the atmosphere. If the moisture gradient to the atmosphere is severe, the seeds may never obtain sufficient moisture to germinate. Remember that most seeds germinate without pretreatment to break dormancy, but all seeds are initially held in a dormant state by desiccation. Moisture relations can impose dormancy upon any seed.

In the humid East and in other areas with growing season precipitation, seeds that require light have a good chance of germination during transitory periods of satisfactory moisture conditions. Even in the arid Southwest, several species of perennial grasses require light for germination, but these species germinate and establish during the summer monsoonal rains. In the portion of the American West where precipitation is restricted to winter months and is largely out of phase with temperatures for plant growth, surface germination becomes extremely hazardous. On disturbed sites with soils with low organic matter content, the risk is increased.

When a seed that requires light for germination is placed in a situation where moisture conditions override the phytochrome response and induce dormancy, the seed remains dormant until a secondary physiological system is triggered that takes over control of germination. Suppose our light-requiring seed that lacked sufficient moisture for germination is gradually buried by litter fall and rain drop splash on its harsh seedbed. Burial blocks the operation of the physiologically active phytochrome system, but the seed is still close enough to the soil surface so that it is exposed to extreme diurnal fluctuations in temperature. As previously noted for seeds of common mullein, the temperature shift may trigger germination in the absence of light and the slight coverage of soil and litter would be sufficient to bring moisture relations into balance and permit germination.

Nitrate

When you work in the field dealing with revegetation of disturbed lands it is common to note a flush of spring germination. Part of this is accounted for by seeds responding to warmer temperatures after prechilling requirements were satisifed. A contributing factor to spring flushes of germination is available nitrate through nitrification. The germination of many dormant seeds is enhanced by available nitrate ion enrichment. Raw, low organic matter content soils on disturbed sites may be so starved for nitrogen that this form of germination enhancement is not available. We know that this is true where you have accumulations of litter under woody plants where the carbon:nitrogen ratio is high (Young and Evans 1975) and have demonstrated in bioassay procedures that germination can be enhanced through nitrate enhancement (Evans and Young 1975). Can germination characteristics be manipulated in seedbeds on disturbed sites through nitrate fertilization? No one, to my knowledge, has conclusively demonstrated that this is possible.

Artificial Seedbeds

It is a huge step to go from the laboratory to actually planting seeds in a seedbed in the field to establish vegetative cover on a disturbed site. Planting seeds is among the most basic instincts of human culture, and millions of subsistence agriculturalists in the Third World are dependent upon this simple task. The planter that has not had a stand failure has never attempted to grow plants from seeds in the field.

The more ecological factors pertaining to seed germination and juvenile seedling growth you control, the less the chance of failure. Ideally you have a weed free, firm but friable seedbed covered with mulch, and control over irrigation, predation, and grazing.

In my experience, the most common sources of seedling stand failure on wildlands are in order of occurrence: 1) seeding too deep; 2) improper seed placement and coverage; 3) competition from weeds; 4) seeding nonadapted species; 5) predation of seeds or seedlings; and 6) natural disasters, floods, drought, or wind erosion.

Technology of Seeding

Before we explore the various hazards to seedling establishment, let us review the necessary steps in seeding technology (Young and Evans 1987). There has to be some method of transporting the seeds as they are planted. Your hand, a coin envelope, the hopper on a hand seeder, or a drill seed box with the capacity of several hundred kilograms of seed serve the same purpose. If seeds of more than one species are being seeded at the same time in a mixture, separate containers for each species or agitation to keep the seeds mixed in the same box are required. If the seeds have fluffy appendages or hairs that can not be removed, special agitators such as arms rotating in the opposite direction are required.

The second technological requirement for seeding is some means of metering the seeds. Obviously an evenly spaced stand is usually most desirable to fully occupy the site and to minimize intraspecific competition. The most common mechanical metering system for planting is a fluted roller or shaft. Occasionally in technologically advanced machines, slotted plates with the slot machined to the size of specific seeds are used. Metering systems are usually driven from traction mechanisms.

If the seeds are to be broadcast on the surface of the seedbed, this is all that is required for mechanical seeding except for some means of distributing the seeds, such as a spinning impeller. If the seeds are actually to be planted in the seedbed, an opener is required. The opener is a fixed shovel, a rolling or a cupped disk, or a fluted colter that forces the soil apart for a small opening or drill for the placement of the seed. For the mechanical drill to function properly there are two other requirements: tubes to transport seeds between the metering device and the opener, and some means of closing the drill opening and covering the seed.

Seeding Depth

The general rule for depth of seeding is two and one half times the diameter of the seed. If you stop and consider this rule, it is obvious that most seeds need to be planted at very shallow depths. In order to accomplish this, the seedbed has to be rather uniform. Lateral variations in topography ruin depth control on a microscale. If you have nearly flat microtopography, the wider the drill the more precise the depth control. The reciprocal is true with uneven microtopography. The most narrow drill, an independently suspended opener, has the potential of providing the most precise depth control with irregular microtopography. Unfortunately, the only depth control for an independently suspended opener is a depth band on the opener.

Remember that some seeds have dormancy systems that require extreme diurnal temperature fluctuations for germination. Soil is an insulator and the deeper the seed burial the less the temperature fluctuation. For the majority of seeds, extreme temperature fluctuations depress rather than enhance germination. Small seeds of this nature can be planted at shallow depths in the bottom of furrows. The furrows serve as microtopography to dampen extremes in diurnal temperatures fluctuations (Evans et al. 1970).

What happens when you are seeding mixtures with different sized seeds? If you only have one box to hold seeds on the drill, the depth setting has to be a compromise. Generally the optimum depth for the dominant species in the mixture is chosen. Drills are now being manufactured with multiple boxes that feed alternate openers that can be set at different depths. The choice of openers and the durability of the mechanism, because of the obvious complexity, may not be suitable for all seeding situations, especially on disturbed lands. Even with the relatively crude rangeland drill, it is possible to vary seeding depth if the drill is equipped with more than one seed box. Larger grass seeds can be seeded through the openers and small seeded legumes or very small seeds of big sagebrush can be dribbled ahead of the opener, perhaps in alternate rows to the grass seeding.

Why are seedings consistently made at too great a depth? Part of the problem is human nature to sock the seeds in the ground so they have a good chance to grow. While conducting research on hydroseeding, I had a revegetation contractor tell me that he could obtain any depth I wanted by just increasing the pressure. We never had the opportunity to check this hypothesis because the pumps used to obtain the pressure largely destroyed seed viability before the seedbed was reached (Kay et al. 1977).

Optimum seed placement implies a balance among contact between soil particles and the seed coat for hydraulic conductivity, adequate soil aeration, and minimal resistance to seedling emergence. Obtaining proper seed placement is often a function of soil moisture content. If the seedbed is too wet, there is the danger of crusting and problems with seed tubes clogging and openers not self cleaning. In wildland seeding on disturbed sites, soil moisture content is much more often a problem. Without supplemental irrigation, contractors are dependent on nature for moisture events. At high elevations the first fall moisture event may be snow that closes the revegetation site. Interesting experiments have been conducted by Hauser (1987) in injecting water through the drill opener to enhance soil-seed contact.

Plant Material for Environmental Restoration

In the past, most of the emphasis on restoration of disturbed lands was to enhance grazing or forestry use of the area. By using well-designed methodology, notable success has been obtained in interseeding shrubs and forbs in grass stands on disturbed sites (e.g., Richardson et al. 1986). With the current interest in biological diversity, longer and more varied species lists are being proposed for restoration of complete communities. We need to give a lot of thought and research effort to the timing and spacing of

these diverse plantings to reduce intraspecific competition among the seeded species.

Competition From Weeds

Remember that in using top soil as a seedbank source you get the bad and the good species. Many weed species have seeds highly adapted to remaining viable for long periods in seedbanks. I am not experienced in seeding mine spoils, but on a variety of wildland situations I have found a season of fallow certainly assists in weed control and ultimately in seedling establishment.

Predation

The key to manipulation of seed predators is habitat changes to reduce predator populations and to encourage predation of the granivorous. The use of repellents on seeds has almost ended because of lack of environmentally acceptable materials. A great deal more research is needed on the influence of granivors on regeneration of native plant species. The influence is not always negative. The regeneration of several species is often tied to scatter hoard caching. Scatter hoard caching consists of multiple caches of small numbers of seeds buried at a shallow depth in the surface soil. Often this type of burial is ideal for cool-moist chilling of seeds and subsequent germination and emergence of seedling. Rodents also cache seeds in larder hoards located in underground burrows. These hoards usually remove seeds from the possibility of germination.

Green Thumbs

Experience is a great teacher in the science and art of revegetation and environmental restoration. Providing a regulatory environment that allows individuals to be innovative is essential for environmental restoration to be successful.

Evaluating Success

The final m`easure of success in terms of seed ecology in environmental restoration is if the reestablished community is successful in renewing itself. Many of the crested wheatgrass *(Agropyron cristatum)* stands in the Great Basin have persisted for four decades with little evidence of aggressive spread or stand renewal. For fully stocked stands there has been no need or environmental potential available for seedling recruitment. However, it is possible to find isolated plants in seedings that were termed unsuccessful, with no progeny evident around the plant. In more favorable environments crested wheatgrass has spread from the sites of original seeding (Hull and Klomp 1967).

At this time there is no estimate of how long these stands of exotic perennial grasses will persist, but it appears that eventually they will be replaced with other species or mixtures of species. How many other artifically revegetated stands of exotic, naturalized, or native species are merely transitory occupiers of the site and eventually through seedling establishment will change in botanical composition?

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Evaluating Community-Level Processes To Determine Reclamation Success

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Abstract

The 1977 Surface Mining Control and Reclamation Act (SMCRA) refers to the reclamation of community level structure and processes in Sec. 515 (19) when it requires the operator to: "establish . . . a diverse, effective, and permanent vegetative cover of the same seasonal variety . . . and capable of self regeneration and plant succession at least equal in extent of cover to the natural vegetation of the native area . . . ." Naturally high levels of diversity can seldom be economically replicated on mined land, but a functional diversity that includes the dominant life forms and plants of varying phenology can be achieved. Within- and between-habitat diversity also need to be considered, as natural landscapes contain heterogeneous patches of vegetation. An effort to simulate natural patchiness may result in more successful reclamation if plant mixtures are chosen for adaptations to microenvironmental conditions. To maximize species diversity and productivity, plants should be chosen to minimize competitive interactions in mixtures. This can be done by choosing species that are different in their temporal and spatial use of resources. The goals of high diversity and high productivity are sometimes at odds, as there are numerous examples of high yielding species that respond to fertilization, and that exclude more slowly growing species. The goal of reclamation is to create communities that are as stable as are undisturbed communities, but there are as yet few examples of stable, artificially reclaimed communities that have also met the criteria of diversity. With time, researchers will be able to test hypotheses concerning stability on older stands. Practicing reclamationists can add to this body of knowledge by creating and measuring communities that are planned using ecological concepts.

Introduction

Many of the measurements that are typically taken to assess reclamation success reflect community-level structure or functioning, including diversity, phenology, stability, production, and others. In fact, the 1977 Surface Mine Control and Reclamation Act (SMCRA, Sec. 515, para. 19) refers to the community level when it requires the mine operator to "establish . . . a diverse, effective, and permanent vegetative cover of the same seasonal variety . . . and capable of self regeneration and plant succession at least equal in extent of cover to the natural vegetation of the native area . . . ." Each of the terms of this paragraph, while written in legal language, refers to various ecological concepts (Table 1). A reanalysis of this language, the implied concepts, and allied concepts that are not directly implied are of value in defining the kinds of measurements that need to be taken. Such a reanalysis is the subject of this paper.

Table 1.—Legal requirements for assessing reclamation success as set forth by SMCRA of 1977, Sec. 515 (19) and ecological concepts that pertain to them

Legal requirement	Ecological concept
Diverse	Species diversity
	Structural diversity
	Species composition
	Dominance
	Rare and uncommon species
Seasonal variety	Phenology
	Life form
Effective, permanent, self-regeneration	Establishment
	Production
	Competition
	Reproduction
	Stability
	Resilience

Some of these measurements (Table 1) do not fall exclusively into the area of community ecology, such as stability, which is also used in an ecosystem sense, or establishment, which is used when discussing individuals or populations. However, ecologists recognize that it is often difficult to draw a line between the processes that occur in populations, communities, and ecosystems, and the intent of the law surely was to promote ecosystem and population as well as community processes. Thus, some of the community processes discussed here will interface with population and ecosystem ecology. Succession will not be covered in this chapter, as it is the subject of the chapter by Chambers, MacMahon, and Wade (this volume).

Both the terms reclamation and restoration are used here, and they are as defined in the introductory chapter. Restoration is the attempt to create identical conditions before and after disturbance, while reclamation is the attempt to create somewhat similar conditions, and may include introduced species.

Diversity

Both structural and species diversity are important considerations for reclamation. Species diversity refers to the number of species (richness) and their relative importance, while structural diversity is the patchiness and vertical distribution of organisms. Species diversity can be measured by alpha, beta, and gamma diversity. Alpha diversity is typically measured by enumerating species richness and eveness with a habitat, patch, or homogeneous land unit (Whittaker 1975). Alpha diversity can be measured using various indices such as H' (Shannon-Wiener diversity index) or S (Simpson's index), and should be similar in the reclaimed and reference areas. In fact, there are questions about what these indices actually measure (Peet 1975; Chambers 1983), and the choice of index needs to be carefully considered to reflect the needs of any comparison, e.g., whether the goal is to have many of the original species or only similarity of the dominant species as in most reclamation projects. A species list with dominance values of individual species should be included when an index of diversity is used for comparison of reclaimed and reference areas, and may often be more effective and more interpretable than an index in determining success.

Beta and gamma diversity incorporate concepts of species and structural diversity (Whittaker 1975; Routledge 1984). Beta diversity describes between-habitat or between-patch diversity, and gamma diversity is known as landscape or total diversity, the sum of the diversity of all the patches. Thus the terms can be used to help describe patchiness or horizontal structure, although not vertical structure. Beta diversity is high if there is low similarity between patches, and is calculated as $\beta = \gamma/\alpha$. Gamma diversity is high if the landscape contains many dissimilar patches. In recent years reclamation plans have begun to call for more than one seed mixture to conform to the different edaphic and topographic characteristics of a site. This is an attempt to increase gamma diversity. DePuit (1984) described topsoiling strategies to increase gamma diversity, such as using different topsoil depths at different locations. Gamma diversity is not only important in assuring a maximum plant species richness on the site, it is extremely important for recolonization of animal species that require different habitat types (Parmenter and MacMahon, this volume). High gamma diversity increases the likelihood that colonizing species will find habitats to which they are adapted. Pre-disturbance and reference area assessments need to incorporate gamma diversity, which can be measured by Simpson's or the Shannon-Wiener indices (Routledge 1984).

Structural diversity includes both vertical and horizontal structure. Large-scale horizontal structure is discussed above as gamma diversity, but small scale structure also needs to be considered. Plants in natural communities form small patches because of initial colonization events, patchiness of resources, clonal growth, and competitive interactions. The dispersion of the patches may be regular, random, or clumped, depending on a number of factors such as age of the stand and interactions between individual species (Pickett and White 1985). One pattern that is important to natural and reclaimed stands is the "islands of fertility" formed by shrubs in desert and semidesert biomes. These islands have an important role in providing nutrients and water to the shrubs because the plants can "mine" the interspaces for available resources (West 1989; Garner and Steinberger 1989). They can also capture dispersing propagules of plants, animals, and microorganisms and thus increase the rate of succession on natural or reclaimed lands (M. Allen 1988a). Standard reclamation practices often obliterate plant structural patterns by drilling seed in rows. Following these practices, the soil resources remain random rather than dispersed, the self-fertilization process does not occur (M. Allen 1988b), and the stand may decline in productivity (Whitford 1988). Thus simulation of natural plant patchiness may be critical to reclamation of productive communities.

Vertical structure can be recreated on disturbed lands by reestablishing the same or similar plant life forms that existed prior to disturbance. Even the simplest communities have vertical structure, and these vary in complexity from deserts and grasslands that have only one or a few layers of vegetation to multi-layered tropical forests. Over- and understorey vegetation may be interdependent, as in the case of shade-dependent seedlings that mature to become sun-dependent trees or of obligately shade loving plants (e.g., Young and Smith 1979). The omission of important plant life forms not only will change community functioning but also is the most obvious error in recreating an estheticially pleasing stand that a reclamationist can make. Creating a grassland where there was once a shrubland or forest brings immediate attention to the inappropriateness of some reclamation practices, and creates an incongruous patch in the landscape. It is not necessary to restore all species to achieve similarity in vertical structure of reclaimed and natural areas, but it is necessary to simulate this structure. This goal can be achieved by choosing representatives of all of the major life forms, e.g., trees, shrubs, grasses, and forbs if these were originally present.

While the goal of restoration is to include as many of the original species as possible, a reclamation plan might include only the dominant plant species. Ideally these would be planted so that they are similar in order of dominance to the reference area, but in reclamation practice this occurs less often than is desirable from an ecological standpoint. A 1988 symposium on reclamation success indicated that most reclamation efforts are still aimed at planting pasture or grassland, even if these were not the original vegetation types (E. Allen 1988).

Rare and uncommon species are seldom considered for

reclamation, even though they are important components of plant communities. There are many rare species, but only a few common ones (Rabinowitz et al. 1986). The uncommon and rare species may, taken as a whole, form a greater proportion of the plant community than many of the abundant species (e.g., Allen and Forman 1976). The abundance of uncommon species is illustrated by dominance-diversity curves from reclaimed and undisturbed Wyoming sagebrush-grassland (Fig. 1). The undisturbed area has many species, but the reclaimed mined site has few. While the reclaimed site has many of the same dominant species as the undisturbed, there are also many missing, such as some of the dominant shrubs.

The dominants that are excluded may in some cases be "keystone species." These are species that control the abundance of important neighboring species, both plants and animals, and thus the functioning of the entire community (Terborgh 1986). Shrubs may be such keystone species in that they create microsites for establishment of other species (e.g., Franco and Nobel 1988) and form the islands of fertility described above. Plants with nitrogen fixing symbionts have a similar keystone role (see paper by Palmer, this volume). The functioning of species that are purposefully excluded from reclamation mixtures must be carefully examined to assure that their absence does not lead to the creation of a community that is entirely different from the reference area or from what is intended.

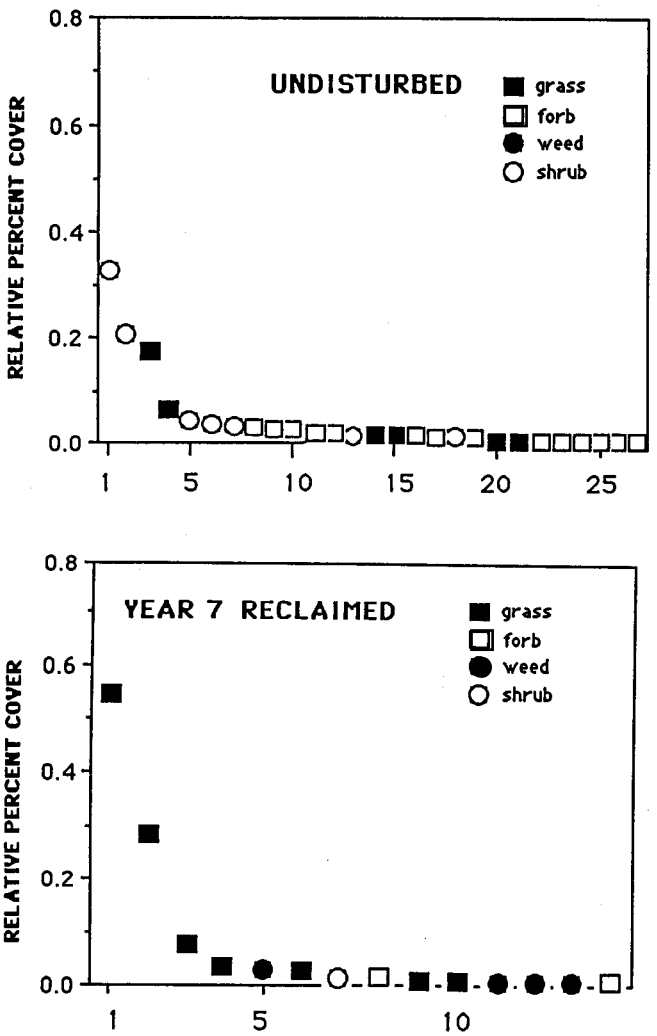

Figure 1.—Dominance diversity curves of 7-year-old reclaimed and native undisturbed areas in Wyoming sagebrush-grassland. The y axis is plotted on a numeric rather than a logarithmic scale show the large number of species that are low in abundance on the undisturbed site. Data from Parmenter et al. (1985).

Uncommon and rare species perform some important functions and should not be overlooked. For instance, all of the leguminous species in the undisturbed areas of Figure 1 are naturally inabundant, yet none has been included in the reclamation mix. Inabundant species are also important to increase diversity. A high diversity of species may help maintain year-to-year and site-to-site productivity, as each species has different responses to environmental conditions and will have the greatest productivity under its peak conditions. In other words, diversity leads to stability. There are many arguments for the maintenance of diversity (e.g., Soule 1986), and restoration has even been suggested as a method to maintain diversity of severely disturbed habitats (Jordan et al. 1988).

However, there are economical and ecological limitations to restoring a high diversity on most sites. One method that has partially overcome the problem is to use the native seedbank in freshly applied topsoil (Bell 1988; Thompson and Wade 1990). Where the seedbank is insufficient the hope is that with natural dispersal and succession, the lesser abundant native species will colonize the site and increase the diversity without the difficulty and expense of planting inabundant species. Colonization has occurred on some sites, as between planted, relatively widely spaced shrubs in a mine restoration project in southwestern Wyoming (West, personal communication), but has not occurred on other sites that used the more typical reclamation practice of densely seeding fast-growing plants that establish rapidly to stabilize the soil (e.g., Bock et al. 1986). The latter practice has the advantage of reducing soil erosion, an understandable goal when the expense of preserving and recontouring the topsoil is considered. However, there is a trade-off in that this aggressive reclamation mixture may preclude establishment of later colonizing species (Bock et al. 1986; Palmer, this volume). A solution to the problem might be to use other methods to stabilize the soil, such as mulching or furrowing, and seeding a more open stand of plants that allows establishment of colonizers. Even this may not always be a viable solution, where the colonizers are undesirable weeds. In general, a site that is rich in soil resources will be low in diversity (Tilman 1987). Reclamationists need to experiment with rates of fertilization and irrigation to achieve the desired diversity. Most often a low or moderate level of fertility will achieve the highest diversity (Powell et al. 1990).

Phenology

The legal requirement for seasonal variety of plants can be interpreted as including plants of varying phenology. One of the most obvious physiological determinants of phenology is made by photosynthetic pathway. Warm season plants have the C_4 photosynthetic pathway, they have relatively high temperature optima for photosynthesis, they are seldom shade tolerant and they photosaturate at light intensities that are somewhat greater than full sunlight, and they have high water use efficiency. Conversely, cool season plants have C_3 photosynthesis, relatively low temperatures for photosynthesis, are often shade tolerant and photosaturate at about one-third of full sunlight, and have low water use efficiency. The Gramineae have more C_4 species than any other family. There are C_4 representatives among forbs and shrubs, especially from arid and semiarid climates, but there are few C_4 trees. This is likely due to the self shading of leaves caused by trees with multilayered canopies, coupled with the lack of shade tolerance.

There appears to be no pattern of drought stress tolerance among C_3 and C_4 plants. In the Nebraska Sandhills the C_3 grasses developed lower xylem water potentials than the C_4 grasses (Barnes and Harrison 1982). There is a larger proportion of C_4 grasses in southern North America. Regression analysis showed this proportion to be best correlated with July temperatures and not at all with precipitation (Teeri and Stowe 1976). However, C_4 grasses only occur in areas that receive summer precipitation or have access to stored soil moisture during the period when temperatures are optimum for photosynthesis.

Within the photosynthetic pathways there are further phenological variations. For instance, there are many shade intolerant, C_3 spring ephemerals that complete their life cycles before the co-occurring tree canopies leaf out. The C_4 shrub *Atriplex confertifolia* has a leaf temperature optimum of only about 25°C, explaining its ability to grow actively both earlier and later in the season than would be expected of a C_4 plant (Caldwell et al. 1977). Thus it is important to know the phenological characteristics of individual species, as well as their photosynthetic pathway, to include a diversity of phenologies in a plant community.

Rooting depth also plays a role in phenology. Shrubs tend to be more deeply rooted than herbaceous plants, and therefore may have greater access to water. This may in part explain the long growing season of *Atriplex confertifolia* in a climate with an arid summer (Caldwell et al. 1977). Phreatophytes, which have their roots in the water table, are capable of season-long growth in arid climates (Nilson et al. 1984).

Plant communities are typically composed of species with varying phenology and life form that are adapted to the local climatic conditions. For instance, in the Chihuahuan Desert, where both summer and winter rains occur, C_4 plants grow in summer while C_3 plants are most active in late winter to early spring (Kemp 1983). Plants that have co-existed for long time periods are thought to have evolved mechanisms to reduce interspecific competition (Pianka 1981). The temporal division of resources that comes with phenological diversity is one likely strategy for achieving reduced competition. The inclusion of species with diverse phenologies will not only assure reduced competition, it will assure maximum utilization of soil resources throughout the growing season. This will then maximize productivity throughout the season, another important goal for reclamation.

Competition

One of the goals of reclamation is to hasten the rate of succession by introducing late seral species. However, colonizing annuals, often weeds, still are part of this process, and they are known to compete with later seral species (Connell and Slatyer 1977; Allen and Knight 1984). Reclaimed sites consist of the juxtaposition of pioneer species with climax species, and are represented by few intermediate stages (E. Allen 1988). In communities with many complex stages of succession, such as eastern deciduous forest, this juxtaposition is not so prevalent naturally, as the pioneer species have often disappeared by the time the late seral species are abundant. However, where the "initial floristics," model applies, or colonization of late seral species in early seral stages occurs (Egler 1954), late and early seral species do interact. This occurs especially in communities with few stages, such as deserts or semideserts, where the late seral species are likely to encounter pioneer species as neighbors even under conditions of natural succession (E. Allen 1988).

I studied the interactions between planted reclamation grasses and colonizing annuals during 1982-1988 in Lincoln County, SW Wyoming. The native vegetation is shrub-steppe and receives 230 mm precipitation annually, about 60 percent as snow. May and June receive the greatest precipitation, with drought typically ending the growing season in July or August. The topography is hilly, and soils tend to be clay loams. More detail on the site description can be obtained in Parmenter et al. (1985). The research area was prepared after coal extraction by regrading the overburden to approximate original contour of 1:5 and 1:6 slopes. Part of the area received 25 cm stored topsoil, and part was left with a subsoil. Native grasses *(Agropyron dasystachyum, A. smithii, A. trachycaulum, A. spicatum)* were seeded in the fall of 1981. Annual weeds, primarily *Salsola kali* and *Bromus tectorum,* colonized naturally in the spring of 1982. Other less abundant weeds include *Amaranthus albus, Chenopodium album, Descurainia sophia, Lepidium perfoliatum,* and *Polygonum arvense.* These all constituted 2 percent or less of the weed cover in any year, while *S. kali* had up to 44 percent cover and *B. tectorum* up to 25 percent. To test the effects of the annuals on grass growth, they were removed by hand from one-half of 144, 0.5 m^2 permanent plots at each of the five sites. See Allen and Allen (1986, 1988) for details on the experimental design.

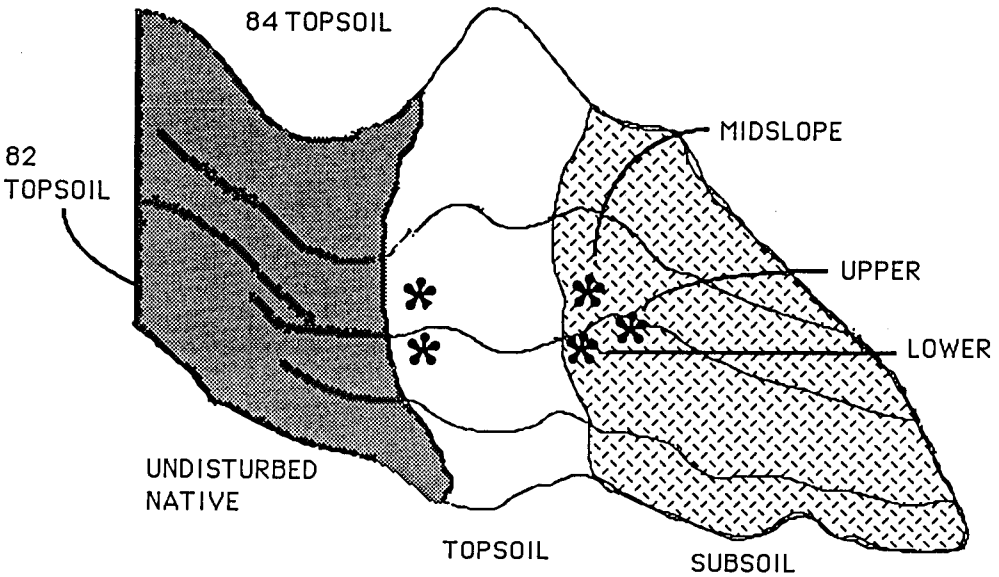

Figure 2.—Locations of the five research sites at the Kemmerer Mine. Three were on subsoil (upper, 1984 midslope, and lower), and two were on topsoil (1982 topsoil, 1984 topsoil). Two of the sites were initiated in 1984, three in 1982.

Five sites were chosen for study, two on topsoil and three on subsoil. The test the effect of year of initiation of succession (and therefore climatic variability), two of the sites, one each on topsoil and subsoil, were initiated in 1984. This was done by discing the site to destroy existing vegetation and reseeding with the same grass mixture in early spring of 1984. A schematic of the area (Fig. 2) shows the relative location of the 1982 and 1984 topsoil sites, the upper and lower subsoil sites, and the midslope 1984 subsoil site.

The patterns of interactions were different among the five sites in that the annuals either competed with, facilitated, or had no effect on the percent cover and density of the planted *Agropyron* grasses (Figs. 3-6). An increase in grass density caused by the presence of annuals was the most frequent occurrence. For instance, the weeds resulted in an increase in both grass density and cover in the upper subsoil site during one or more years (Fig. 3). This indicated that the annuals were nurse plants for the establishing grasses, or in other words facilitated grass growth. This occurred because the dominant annual was the tumbleweed *Salsola kali,* which remains on the site as a litter cover during the winter. Where it was not removed as part of the experimental treatment, it caused increased snow capture and provided an improved microenvironment for grass establishment during the spring (Allen and Allen 1988). Grass density was higher where weeds were present by the second growing season, but it took several years before grass percent cover was also improved (Fig. 3).

Grass density was also improved by the presence of *S. kali* in the lower subsoil and 1982 topsoil sites (Figs. 4 and 5). However, there was no change in percent cover of the grasses at either of these sites. Apparently, the less dense grass individuals were able to compensate for lower density by greater growth on these two sites.

An entirely different pattern was observed at the 1984 topsoil site, where the percent cover of the grasses was decreased by the presence of annuals by the final year of measurement, or in other words they experienced competition from the annuals (Fig. 6). The grass density was not significantly affected at this site, although in 1984 and 1987 grass density was higher in the weed removal plots at $p = 0.08$. The reason for this different pattern may be that *Bromus tectorum* became the most abundant annual weed at this site after a few years, although *S. kali* colonized in the early years. (The unusually high colonization of *B. tectorum* at this site is likely due to its proximity to the native unmined area, where previous grazing disturbances had resulted in colonization. At all the other research sites, it had less than 2 percent cover).

Unlike the later growing C_4 *S. kali, B. tectorum* is C_3 as are the *Agropyron* species During some years *B. tectorum* germinated in fall and survived the winter even in this cold climate, and apparently competed with *Agropyron* species and reduced the growth of the perennial grasses the next spring. This pattern of competition between *B. tectorum and A. spicatum* was also noted by Harris (1967).

The final pattern of interaction was observed at the 1984 midslope subsoil site (data not shown), where there were no significant effects of the annuals on *Agropyron* species density or percent cover. A summary of the effects of the annuals on the five sites is shown in Table 2. Facilitation

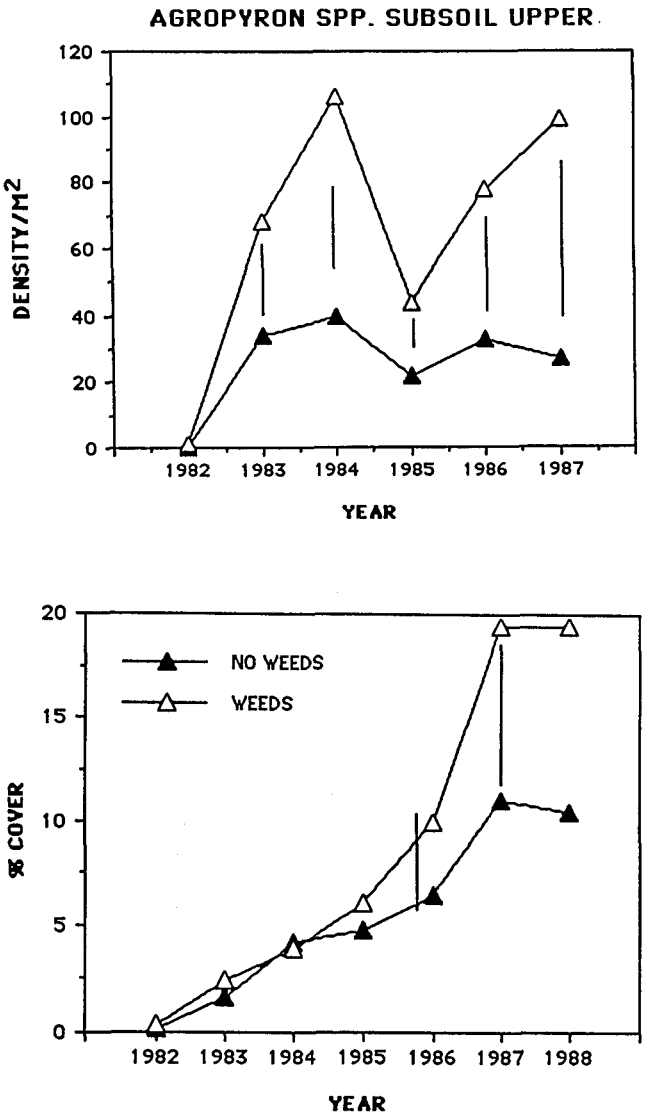

Figure 3.—Density and percent cover of the four planted species of *Agropyron* on the upper site (subsoil) with and without annual weeds from 1982-88. Individual grasses were difficult to distinguish after 1987 and were not counted. Weeds were removed by hand to create the "no weed" treatment.

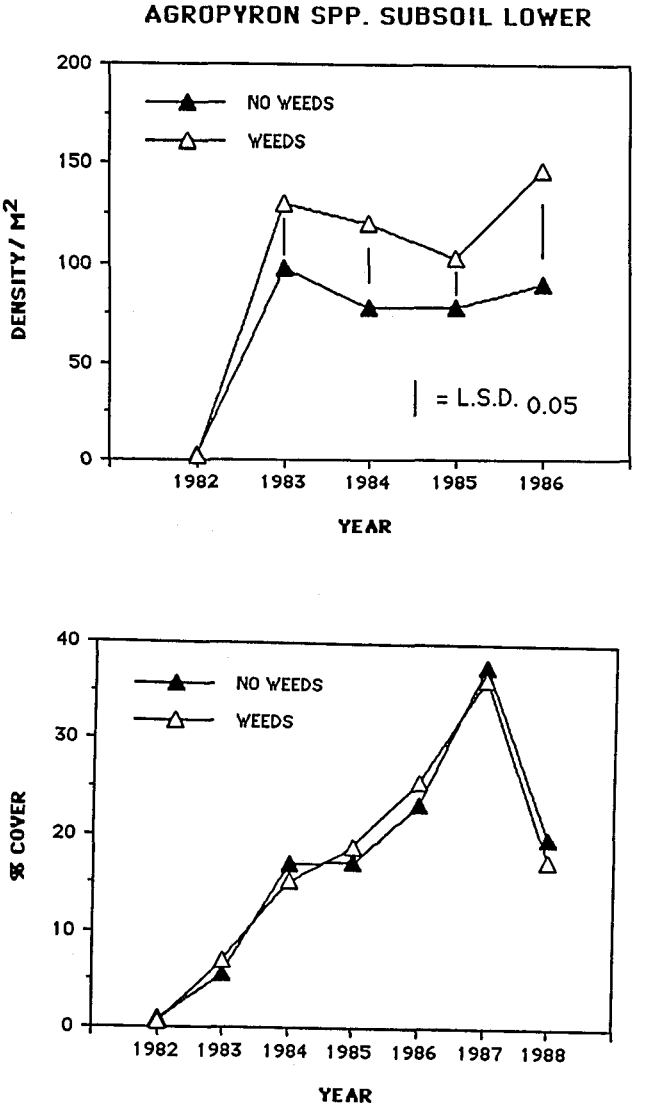

Figure 4.—Density and percent cover of the four planted species of *Agropyron* on the lower site (subsoil) with and without annual weeds from 1982-88. Individual grasses were difficult to distinguish after 1986 and were not counted.

Table 2.—Effects of annual weeds on density and percent cover of *Agropyron* species

Item	*Agropyron* density	*Agropyron* cover
Increase (Facilitation)	1982 Topsoil Upper subsoil Lower subsoil	Upper subsoil
No charge (Tolerance)	Midslope subsoil	1982 Topsoil Lower subsoil Midslope subsoil
Decrease (Competition)	1984 Topsoil	1984 Topsoil

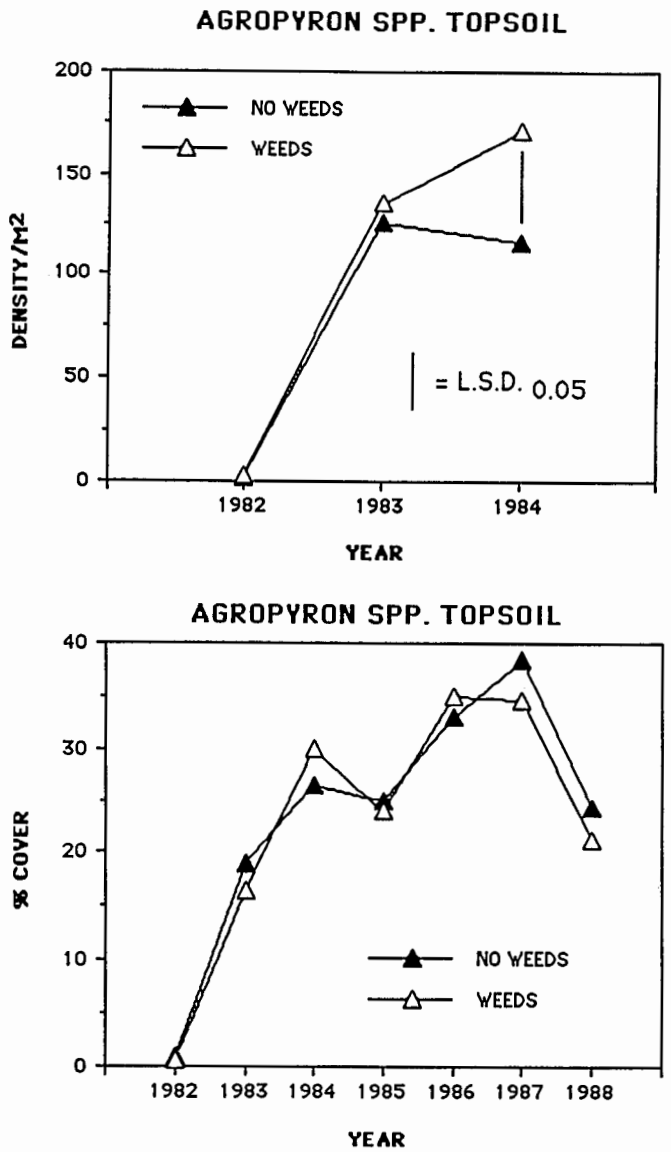

Figure 5.—Density and percent cover of the four planted species of *Agropyron* on the 1982 topsoil site with and without annual weeds from 1982-88. Individual grasses were difficult to distinguish after 1984 and were not counted.

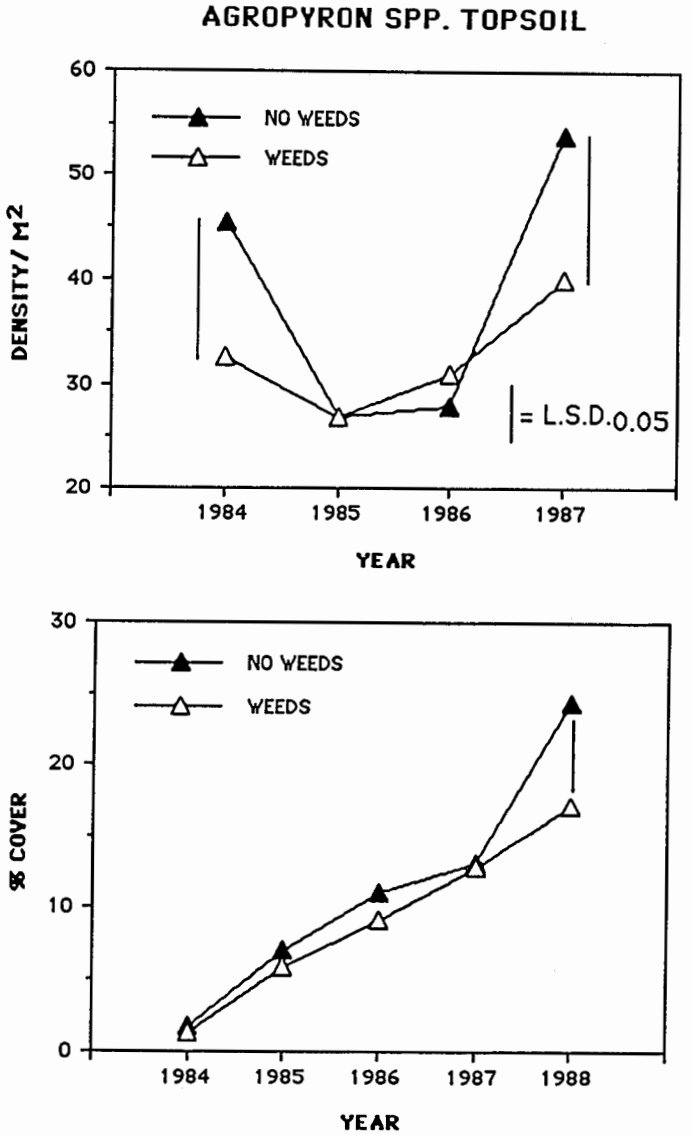

Figure 6.—Density and percent cover of the four planted species of *Agropyron* on the 1984 topsoil site with and without annual weeds from 1984-88. Individual grasses were difficult to distinguish after 1987 and were not counted.

was the most frequent interaction when grass density was measured, but no change was observed most frequently when percent cover was measured. Again, this occurred because the grasses that had decreased density without annuals (facilitation) were able to compensate by producing increased cover per individual.

The general patterns of annual weed colonization are shown in Figures 7 and 8. The upper and lower subsoil sites had an increase primarily in *S. kali* in the early years and then a decline, although the annuals were much more abundant in the upper plot. *S. kali* was virtually the only annual to increase again after 1985 in the upper site, but was only one of 13 species in the lower site, each with about 1 percent cover, after 1984, and the 1984 topsoil site *S. kali* dominated until 1985, and then *B. tectorum* became the dominant annual (see Allen and Allen 1986, 1988 for more details).

The main point for reclamationists to be aware of is that weedy colonizing annuals do not necessarily indicate failure, and may in some situations contribute to the success of reclamation where they facilitate establishment of desirable plants.

These patterns of facilitation, competition and tolerance between planted grasses and colonizing annuals indicate that the interactions are complex, and make the effects of weeds quite difficult to predict. The major pattern that emerges in that if *S. kali* was the dominant weed, facilitation or tolerance were operative. If *B. tectorum* were dominant, competition was observed. These results differ from those observed in eastern Wyoming in disced sagebrush grassland, where *S. kali* competed with seral species that included grasses and native annuals (Allen and Knight 1984). The main differences between the two studies are that the densities and percent cover of *S. kali* and the seral

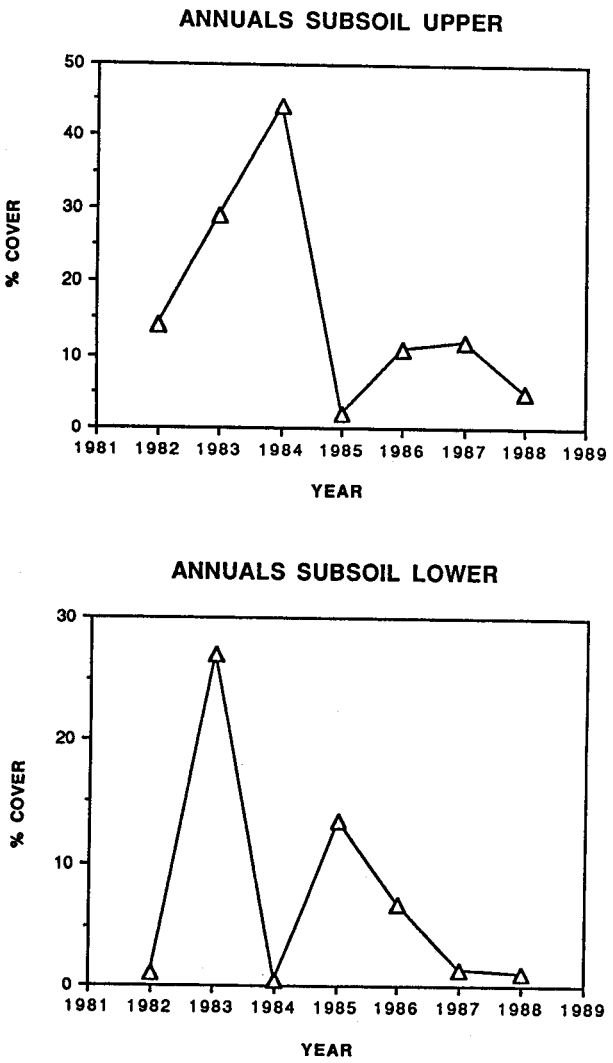

Figure 7.—Percent cover of annual weeds on the upper and lower subsoil sites between 1982 and 1988.

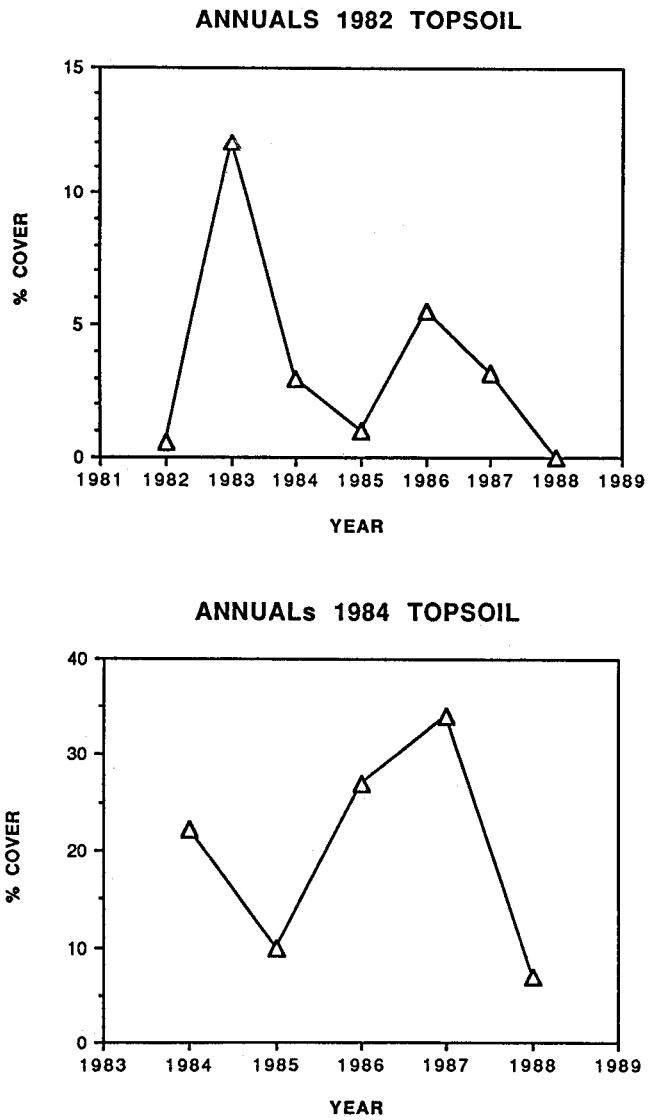

Figure 8.—Percent cover of annual weeds on the 1982 and 1984 topsoil sites until 1988.

species were higher in the moister climate, longer growing season, and richer soils of eastern Wyoming. *Salsola kali* may act to facilitate grass growth if it is relatively low in abundance, as in the study reported here, but it may have the net effect of competing with neighboring plants where its abundance is high.

Stability

Stability has two definitions, and has been divided into resilience stability, the ability of a disturbed site to return to a predisturbance state, and resistance stability or inertia, the ability of a site to resist change after a disturbance (Westman 1978; Fig. 9). Reclaimed sites are often not designed to return precisely to a predisturbance state, as a low diversity of native species, or introduced species are planted. Thus the resilience of the reclaimed sites is low. Whether they have functional resilience, e.g., whether nutrient cycling and other aspects of ecosystem functioning return to a former state, is an open question. A restored site, on the other hand, by definition has high resilience if the restoration is successful.

The question of resistance or inertia of reclaimed lands to minor disturbances is also open. The SMCRA requires 5 or 10 years to determine whether the vegetation exhibits resistance, but a decline after this time period is possible. An interesting example can be taken from the competition data presented above. Both the lower subsoil and the 1982 topsoil sites had a decline in percent cover of *Agropyron* species between 1987 and 1988 (Figs. 4 and 5). This decline cannot be ascribed to climatic variation, as the younger 1984 topsoil site had a continued increase in percent cover in 1988. Whitford (1988) and Palmer (this volume) have suggested the reasons for a decline in productivity after several years may be related to nutrient cycling. If plant litter accumulates over time, nitrogen and other nutrients are immobilized both in the undecomposed vegetation and in saprophytic microorganisms. Densities of microorganisms and available nutrients declined over time in the studies of Whitford (1988) and Palmer. A visual inspection of the two sites described in Figures 4 and 5 showed a dense litter layer on the ground, although data on nutrient immobilization were not obtained. In any case, both sites showed a decline in productivity by the seventh growing season, well before the 10 years required for legal reclamation success, and after seven years standing crop was not as high as in the adjacent undisturbed native area (Waaland and Allen 1987). Further observations are necessary to determine whether productivity would increase again after seven years.

To date, reclamation success has been legally declared on few mined areas (Allen 1988). Thus, I will draw examples of long term stability from other sources of literature. These are older planted stands that have shown stability for up to 40 years (e.g., Bock et al. 1986; Johnson 1986), but these typically have few species or consist only of introduced species and would not meet present day legal requirements. In most cases the lifespan of the planted perennials has not been exceeded, so the longevity of the stand beyond the longevity of the planted individuals is not known. For instance, if a plant survives 50 years, the individuals may be considered established, but the stand is not established unless mortality is replaced by reproduction. In a young stand on an abandoned oil drill pad in arctic tundra (about 5 years old), mortality was high, but was compensated by reproduction. However, plant density was not as high as in the adjacent undisturbed areas (Gartner et al. 1983; Bishop and Chapin 1989). The most hopeful predictions for long-term stability come from prairie restoration projects. The Curtis Priarie at the University of Wisconsin was established more than 50 years ago, and has been a site of intensive study. It shows similarity in structure and functioning to unplowed prairie

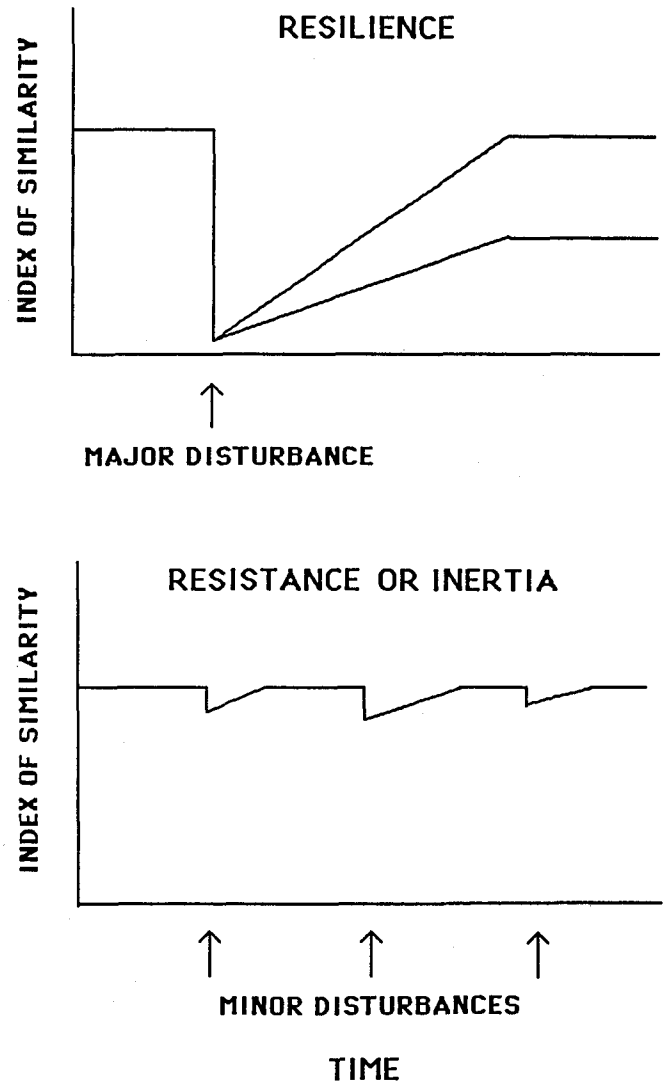

Figure 9.—Diagram of resistance and resilience stability. Resilience means that the site can be returned to a pre-disturbance structure and functioning as measured by a similarity index. Resistance means that the site can recover from a perturbation, often associatied with smaller disturbances than surface mining.

Table 3.—Measurements commonly used to determine the success of reclaimed community structure, and the functional measurements that are needed

What is measured (structure)	What is needed to determine functioning
Production (g/m²)	Productivity (g/m²/yr)
Density	Turnover (mortality, reproduction)
Species richness	Potential functional loss caused by missing species.
"Seasonal variety" of species	Changes in function caused by absence of some phenologies
Number of life forms	Changes in function caused by absence of some life forms
Indices of diversity, similarity	More specific information on species composition, and relationship to functioning
Production, density during 2-3 years	Long-term stability

remnants, and has exhibited resilience for many years (Cottam 1987). Whether reclamation projects with less intensive input and management can meet this impressive goal remains to be seen.

Conclusions

Ecologists have spent much effort in relating community and ecosystem structure to functioning. Structural measurements are preferable because they are usually simpler and quicker to take than measurements of functioning, and they are the types of measurements that are legally required (Table 3). The assessment of reclamation success will provide practical opportunities to determine if and when this relationship exists. For instance, plant density is a required measurement for shrubs and trees, but does not indicate rate of turnover. Reclaimed stands that have adequate density of long-lived plants will persist only for the lifespan of those plants, if they cannot reproduce on the site. Reduced species diversity is a characteristic of reclaimed stands, but normal functioning to maintain long-term stability is expected. If the proper vertical and horizontal structure has been recreated from a limited species pool, and species with important functions such as N fixation are included, then a functioning community may reestablish.

There are many functional attributes of reclaimed communities for which no structural measurements are required (Table 4). Again, the hope is that the structural measurements can be further extrapolated to relate to all important aspects of funtioning. Whether the communities function in the manner designed by reclamationists can only be determined with experimentation and observation over time. However, many basic ecological principles are accepted among ecologists and can be applied in the design of reclaimed sites. Where a self-perpetuating community that resembles the native community is to be created, reclamationists can help assure long-term stability by applying the following principles:

- Simulate gamma or landscape diversity of the reference area in the reclaimed site.
- Simulate smaller scale patchiness of species.
- Re-create a similar horizontal structure by introducing he same or similar lifeforms.
- Include species with varying phenologies to decrease temporal overlap in resource use and to maximize resource utilization throughout the growing season.
- Include known keystone plant species in mixtures, e.g., shrubs that provide microsites for later plant establishment.
- Include some uncommon species in mixtures that have important functions, e.g., nitrogen fixation, that will increase diversity.
- Use species mixtures and cultural techniques that will allow natural plant colonization to increase diversity.
- Take advantage of non-aggressive weedy colonizers that may facilitate establishment of desirable species—control only those weeds that are known competitors.

Table 4.—Structure and functioning for which measurements are not legally required to determine reclamation success

Diversity of horizontal structure (patches and landscapes)
Diversity of vertical structure
Root architecture
Trophic structure
Species turnover
Species interactions (competition, facilitation, symbioses)
Recolonization by animals and resultant composition
Recolonization by microorganisms and resultant composition
Ecosystem functioning: nutrient cycling, mineralization, immobilization, etc.

By following some of these simple steps toward recreating reclaimed communities, reclamationists can likely increase the success of reclamation. Such steps should be coupled with increased monitoring to provide better information to plan for the success of future projects.

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Differences in Successional Processes Among Biomes: Importance in Obtaining and Evaluating Reclamation Success

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Introduction

Following disturbance land undergoes a "repair" process that is termed succession. Because of the universality of this process, the concepts of succession are central to any discussion of land reclamation—a form of managed succession. The rate and direction is affected by a variety of abiotic and biotic processes. In contrast to natural succession, the reclamation of disturbed areas is under some degree of control of humans. The key is in knowing, for any given disturbance, what effects inputs of the reclamationist have on these processes and, consequently, on trajectories and outcomes of succession. This information gives reclamationists the ability to select the most appropriate end land use and to "direct" successional processes towards development of ecosystems that support that land use. It also provides an objective basis for evaluating whether or not reclamation success has been achieved and, in some instances, indicates the best measures of success.

We define succession simply as the change in physiognomy, species composition, or proportion of species on a plot of ground over a moderate time interval (decades to a few centuries) following a disturbance to that site (MacMahon 1980). Relationships among the factors and processes that affect succession and the manner in which they influence succession are summarized in the flow diagram developed by H.S. Horn and J.F. Franklin (1981) (Fig. 1). Many of these factors or processes have been discussed in detail in the previous chapters in terms of how they relate to the reclamation of disturbed lands and reclamation success.

Successional processes span all levels of organization (molecular to biome). Herein, we have chosen to address successional processes at a very general level—that of the biome. Successional processes common to six major biomes are reviewed and differences among those biomes are examined. The manner in which these differences influence inputs of reclamationists and consequent successional outcomes is then explored. Finally, we examine whether current concepts of reclamation success are appropriate given the differences in successional processes among biomes.

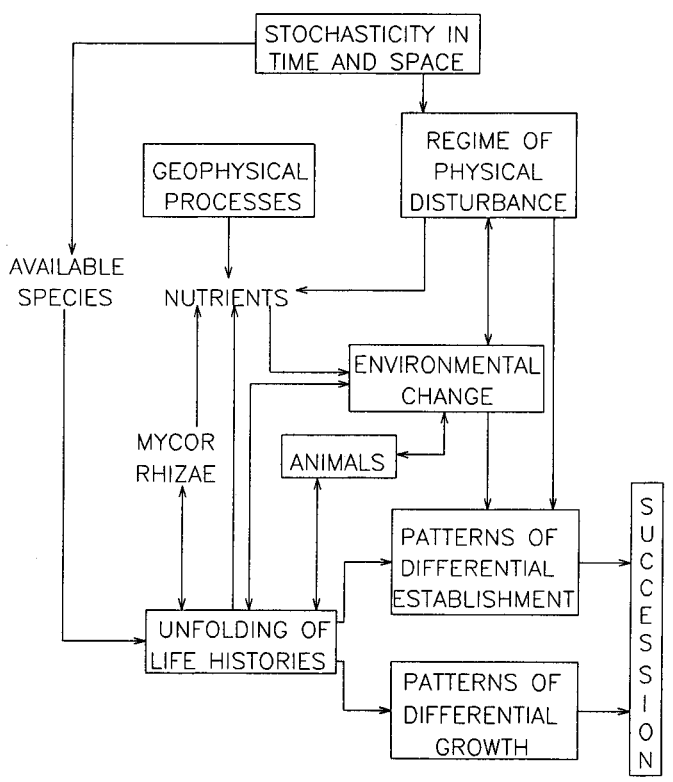

Figure 1.—Flow diagram of major elements with current concepts of succession (compiled and arranged by H.S. Horn and J.F. Franklin).

Successional Processes Common to all Biomes

Clements (1916) accurately portrayed the three major phases and six essential processes of succession early in the twentieth century (MacMahon 1980, 1981; Pickett et al. 1987). In his original description of succession, Clements (1916) stated that secondary succession begins with the "initiation" phase through some type of disturbance and ends with the development of a "climax formation." The processes involved depend upon the type of disturbance (nudation), the propagules remaining in the soil following disturbance and the colonizers that reach the site (migration), the success of the propagules and colonizers in establishment and growth (ecesis), and the alteration of the abiotic environment by these individuals (reaction). During the "continuation" phase species compete with one another (competition) and this results in an additional alteration of the environment. The end result of these processes, the "climax formation," occurs when the mix of species on the site tends to persist for long periods of time. A schematic diagram of succession applicable to many natural systems is presented to illustrate relationships among the stages of succession and the various processes that are involved in succession (Fig. 2).

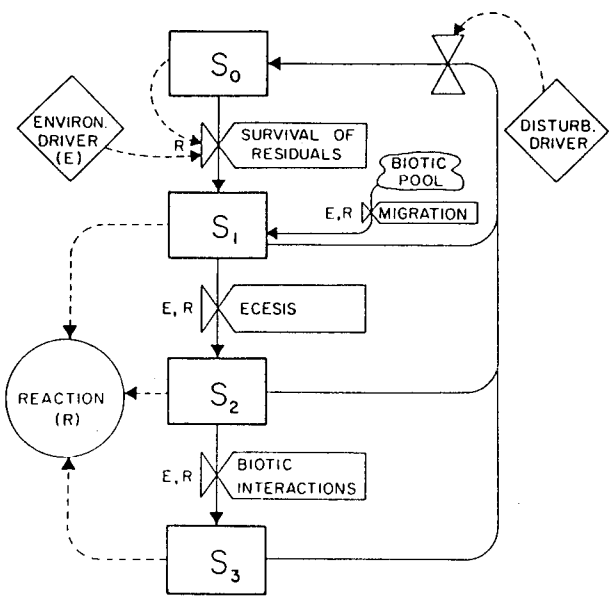

Figure 2.—Model of status of components (organisms and the physical and chemical and physical conditions) of a plot of ground over time. Boxes are states of the plot at any instant. Diamonds are system drivers. The circle is an intermediate variable. Dashed arrows represent information flows. Letters next to the control gates replace dotted lines from that point to the control for graphic simplicity (from MacMahon 1980).

Successional Processes and Reclamati in Different Biomes

A generalized comparison of the differences in successional processes across the various biomes is presented in Table 1. A detailed description of how the information for this figure was compiled is given in MacMahon 1981. It has been updated for inclusion here.

We recognize that exceptions to the comparisons presented exist and emphasize that our purpose is an examination of general patterns. Since we assert that the basic processes of succession parallel the processes required for land reclamation (MacMahon 1987; Redente and DePuit 1988), we discuss the differences in reclamation methodology among biomes as they are dictated by differences in successional processes.

Desert

Desert communities are highly responsive to the climate regime under which they grow (Turner 1990). Periods of mortality are often correlated with prolonged or extreme drought and episodes of establishment are related to unusually heavy precipitation during certain seasons (Turner 1990; MacMahon and Schimpf 1981). Fires are infrequent and usually occur only after a period of above-average rainfall and a buildup of plant fuels (Humphrey 1974). Wind is an everpresent factor and, consequently, plants are adapted to it. Localized mortality may result from outbreaks of pathogens or herbivores.

Because deserts are characterized not only by low but also by highly variable precipitation (MacMahon 1981), plant species adapted to the harsh environment are limited in number. Consequently, the species pool for colonization is often small. Although annual species may be abundant, their density and production is dependent not only upon soil moisture but also upon the relationship between soil moisture and soil nitrogen (Gutierrez and Whitford 1987). Seed production is highly variable among years. Seeds may be dispersed or consumed by rodents, birds, or ants (Reichman 1979; Parmenter et al. 1984; Morton 1985). The final distribution of dispersed seeds both on the soil surface and in the soil seedbank can be highly dependent upon vegetation structure and topography (Price and Reichman 1987). A high correlation between the seed bank and vegetation may exist because of extreme and unpredictable variations in growing conditions and the effects of seed predation (Henderson et al. 1988). Many succulents establish underneath existing "nurse" plants, probably due to more favorable temperature and nutrient relations, even though seedling competition for water with "nurse" plants and shading may result in lower growth rates (Franco and Nobel 1988).

In desert ecosystems species composition and overall physiognomy may be slow to change (Goldberg and Turner 1986). The initial colonizers may persist for long periods of time and the attainment of "climax" following disturbance may appear to be fairly rapid—40 to 100 years (Vasek et al.

Table 1.—Comparison of differences in successional processes involving plants among various biomes. Comparisons include nudation, most important factors creating disturbances; migration, the major types of plant propagules colonizing the site; competition, relative importance of different resources; reaction, degree to which seral biota (plants) alters chemical and physical environment of a site; stabilization, rate at which physiognomy (but not necessarily the composition) of biota (plants) on the site stabilizes; miscellany, degree of physiognomic and species turnover during succession (Revised from MacMahon 1981)

Item	Desert	Tundra	Grassland	Coniferous forest	Deciduous forest	Rain forest
Nudation	Drought	Cryo planation/ burrowing	Fire	Fire/ wind	Wind/ senescence	Senescence/ wind
Migration	Seeds	Nonseeds/ seeds	Seeds and nonseeds	Seeds and nonseeds	Seeds and nonseeds	Seeds and nonseeds
Ecesis	Periodic	Slow-periodic	Moderately fast	Mod fast (variable)	Fast	Very fast
Competition	Water/ nutrients	Nutrients/ water	Water/ nutrients/ light	Light/ water/ nutrients	Light/ nutrients	Light/ nutrients
Reaction	Moderately low	Moderately low	Moderate	Moderately high	High	Very high
Stabilization	Fast	Fast	Moderately Fast	Slow	Slow	Moderately Slow
Miscellany	No physiog. No species	No physiog. No species	Mod physiog. Mod species	High physiog. High species	High physiog. High species	High physiog. High species

1975; Webb et al. 1986; Webb et al. 1987). Depending upon the vegetation assemblage and the severity of disturbance, primarily the degree to which the soils are altered, the dominant species may or may not be the same (Prose et al. 1987; Webb et al. 1987). The overall severity of the site may also determine the degree of physiognomic change. Due to low plant cover and production, reaction or change in the physical or chemical environment is dominated by the effects of individual plants. Scattered vegetation results in "islands of fertility" that are associated with nitrogen accumulation and nitrogen availability (West and Klemmedson 1978). Plant competition varies depending upon water availability. On extreme desert sites plants may never attain densities sufficient to compete.

In the reclamation of desert areas, the highly variable seed supply and low seedling establishment rates necessitate addition of viable propagules of the desired species. Since adapted plant materials are often unavailable commercially, it is usually necessary to collect seeds of the desired species on or near the disturbed area. Several reclamation techniques can be used to improve water relations. Topographic contours can be manipulated to concentrate precipitation, and topdressing materials can be used that allow water infiltration, reduce evaporation, and have high water holding capacities (Aldon and Oaks 1982). Planting schemes can be designed to take advantage of seasonality of precipitation. In areas that receive less than 250 mm of annual precipitation, irrigation can be used to enhance establishment of shrubs and perennial grasses and forbs (DePuit et al. 1982). Irrigation can increase the number and productivity of individual plants that establish (Hunter et al. 1980) and the number of species that establish during a given time interval (Redente and DePuit 1988). In some cases it may be advantageous to accelerate the critical establishment phase through the use of tublings.

Tundra

Small-scale soil movements are the most common forms of disturbance in tundra ecosystems. These occur primarily via cryoturbation processes (Johnson and Billings 1962) and small mammal burrowing (Thorn 1982). Fire and wind are seldom important and the effects of herbivores are often highly localized.

Plant establishment occurs from both seeds and vegetative propagules (Bliss 1985; Chambers et al. 1990). The low heat budgets that characterize tundra ecosystems result in short growing seasons during which temperatures often drop below freezing. Highly variable and generally low seed production (Chambers 1989) and a limited number of seed "safe sites" (Chambers et al. 1991) contribute to low, possibly episodic, seedling establishment. Seed banks of

both alpine and arctic tundra appear to be comparable in size to those of temperate forests (McGraw And Vavrek 1989). Seed production and longevity varies among species (Chambers 1989) and the resemblance of the seed bank and standing vegetation is also variable (McGraw and Vavrek 1989). Seedling mortality is generally high (Bliss 1985, but see Chambers et al. 1990) and may result from needle-ice activity (Roach and Marchand 1984), soil drought, or slow seedling development (Bell and Bliss 1980).

As in deserts, the pool of species adapted to the extreme environments is small. In tundra ecosystems there are few annual species (Bliss 1985) and long-lived perennials are the most stable component. Although definite shifts in species composition occur during succession, once establishment occurs many of the "climax" species are in place (Bliss et al. 1973), a case of "autosuccession" *sensu* Whittaker 1974. Tundra species are low in stature and community physiognomy changes little during succession.

Tundra plants can alter their environment by moderating temperatures within their own canopies and insulating the soil surface from temperature extremes. Because of the generally cold temperatures, most processes, such as decomposition, occur at slower rates than in temperate systems. Competition may involve both nutrient and water availability (Gartner et al. 1983; Johnson and Caldwell 1975).

Several factors must be considered in the reclamation of disturbed tundra ecosystems. Depending upon the size of the disturbed area, residuals and migrants from surrounding native areas seldom result in plant densities sufficient for immediate soil stabilization, even with direct replacement of topsoil. In both deserts and tundra seeds may be redistributed by the wind following initial contact with the soil (Chambers et al. 1991). In wind dominated tundra ecosystems it is often necessary to hold both soils and seeds in place with stabilizing mulches (Chambers et al. 1990). Organic mulches can ameliorate the microenvironment by increasing soil temperatures and soil water and decreasing the deleterious effects of wind (Cochran 1969). Fertilization can increase seedling growth in nutrient poor environments, but may result in a short-duration nutrient pulse in poorly developed mineral soils (Chambers et al. 1990). Also, high nutrient levels may result in high seedling competition in well-developed soils (Gartner et al. 1983). To obtain plant materials adapted to the harsh environment, it is often necessary to collect them on or near the disturbed area. Because plant growth is slow, it may be necessary to transplant established seedlings or plants in areas where immediate erosion control is a reclamation goal.

Grassland

Major and frequent disturbances in grasslands include both fire and drought. Herbivores can effect long-term changes in species composition and create small-scale disturbances (Huntley and Inouye 1988). Seed production is abundant except during droughts (Rice 1989). Seed banks often exhibit strong seasonality and spatial variability (Hassan and West 1986) and there are often significant differences between the seed bank flora and above ground plant community. Depending upon the length of time since disturbance, an abundance of both early seral natives and exotics may persist in the seedbank (Rice 1989). Because of the nature of the seed bank, it may be difficult to assess the composition of the flora that will regenerate following disturbance (Douglas 1965). Establishment occurs rapidly, depending on the scale of disturbance, and may be from residuals or sexual propagules dispersed by wind or animals to the site. During the reaction phase significant changes in soils and microclimate may occur (Hinds and Van Dyne 1980). Rapid growth of above ground plant parts results in shading and competition for light. Nutrient availability is a system attribute that is often closely linked to competition (Tilman 1988). Competition for water, although less than in deserts, may be intense during droughts. Relationships between water and nutrient availability can have significant impacts on competition and, consequently, on successional trajectories (Walker 1981). During succession moderate species turnover and physiognomic changes occur (Weaver 1954) and attainment of "climax" may require several decades.

In the reclamation of disturbed grassland areas it is seldom possible to depend solely upon seed reserves or propagules in topsoil. Since soil seed banks are frequently comprised primarily of early seral or exotic species (Douglas 1965), it is often necessary to seed more desirable or later seral species. On reclaimed areas late seral species may have to compete for resources with naturally occurring early seral species, exotics, or cultivated species that are seeded to hasten the stabilization of the site. Early seral species frequently exhibit higher growth rates, lower root-to-plant ratios, and higher nutrient uptake efficiencies than late seral species (Grime 1979; Chapin 1980). Many exotic species naturally exhibit these characteristics and cultivated species are often bred for these traits. Under the proper growing conditions, these species have highly positive growth responses to nitrogen and phosphorus fertilization (e.g., Aldon et al. 1976; DePuit et al. 1978). At high rates of fertilization or high nutrient levels in general, species that exhibit the greatest growth response tend to outcompete slower growing species (DePuit and Coenenberg 1979; Berg 1980).

Reclamation strategies can attempt to mediate resource competition by careful selection of seeded or planted species, modifying nutrient availability, or direct manipulation of species that are planted or become established on the site (Redente and DePuit 1988). The numbers of highly competitive species that are seeded can be reduced and those that are included can be seeded at lower rates. Less competitive species and species that are difficult to establish from seed can be transplanted onto the site. Fertilizer can be omitted or applied at moderate levels and, if necessary, herbicide or other specific plant removal methods can be used to eliminate or decrease the densities of extremely competitive species.

Coniferous Forest

The primary natural agents of change in coniferous forest are fire (Heinselman 1981), wind (Sprugel 1976), insects, or pathogens, which are often carried by an insect vector (Barbosa and Schultz 1987). Regeneration of disturbed areas occurs from residual seeds, vegetative propagules, and animal dispersed dissemules (Archibold 1979; Van Cleve and Viereck 1981). Seed production often exhibits high periodicity. Coniferous forests tend to be characterized by trees that are either dispersed by wind or cache-boarding mammals and birds (Fenner 1985). Many late seral conifer species are wind dispersed. There is frequently low correspondence between the composition of the seedbank and that of the vegetation (Archibold 1989). Late seral forest species often have low seed longevity and early seral species are often as or more abundant in the seed bank than late seral species in all stages of succession (Archibold 1989). Initial seedbed conditions can have a significant effect on seedling establishment. For certain forest species, establishment may be higher on fallen logs than on soil, apparently due to decreased competition from herbs and mosses (Harmon and Franklin 1989). In cool temperate areas, soil moisture and temperature relations are critical determinants of seedling establishment. Frost-heave and soil drought are primary causes of seedling mortality, especially of late seral forest species. Initial colonizers of severe disturbances are usually herbs and shrubs that are often rapidly topped by fast-growing deciduous tree species (Schimpf et al. 1980; Heinselman 1981; Van Cleve and Viereck 1981; Walker and Chapin 1986). Some conifer species exhibit slow growth rates and higher shade tolerance. Consequently, they may be able to establish in later seral stages (Walker and Chapin 1986) or persist as understory species established early in the successional sere (Bergeron and Dubuc 1989).

Depending upon the severity of the disturbance, significant changes in microclimate and in soil properties occur during succession (Vitousek and White 1981; Vitousek 1985). Plants in coniferous forests may compete for light, water, or nutrients. Shade tolerance has been equated primarily with late seral species and intolerance with early seral species in all forested biomes (Oliver 1981). The degree to which a species responds to shade determines its successional role can be mediated by the availability of other resources. It has been suggested that within a given ecosystem temporal changes in species composition occur primarily in response to autogenic or internal changes in light availability (Smith and Huston 1989). Species zonation or differences among areas has been interpreted as spatial changes in species composition that occur primarily in response to the effect of allogenic or external changes in resource availability on the dynamics of competition for light. In coniferous forests of the Pacific Northwest, shade intolerant species such as *Pseudotsuga menziesii* can form a stable climax if environmental conditions exclude the more shade tolerant species (Franklin and Hemstrom 1981). If environmental conditions favor the more tolerant species, they may dominate in both early and late succession. Several pine species in the southeastern United States exhibit a similar pattern (Smith and Huston 1989). In the absence of fire, they are replaced by hardwoods on more favorable sites but persist and dominate on exposed sites with xeric moisture regimes.

If the conifers are slow to assume dominance over broadleaf early seral stages, there is strong physiognomic contrast between early and late succession. Because of the length of time required for the conifers to assume dominance in boreal, temperate, and subalpine forests, it may take centuries or even more than a thousand years to reach "climax" (Van Cleve and Vierick 1981; Franklin and Hemstrom 1981; Schimpf et al. 1980). However, warm temperate forests may require much shorter times to obtain "climax" (Christensen and Peet 1981).

Since late seral species are often difficult to establish, reclamation of severely disturbed coniferous ecosystems requires creating an adequate seedbed and providing a seed or propagule source. Although it may be desirable to reduce competition, nurse species that ameliorate the environment or maintain required mycorrhizae or other symbiotic soil microflora should be present. For example, the early successional hardwood shrubs madrone and manzanita form ectomycorrhizal associations with some of the same fungal species required for establishment of Douglas fir seedlings in Oregon. If the hardwoods are absent, Douglas fir is often unable to reestablish after severe disturbance (Perry et al. 1989).

In the natural regeneration of these systems, soil conditions are often moderated by the initial colonizers or early seral species (Connell and Slatyer 1977). During reclamation it is frequently necessary to ameliorate the soil environment with natural or artificial mulches (Cochran 1969). Late seral forest species often exhibit significant lag times between seedling establishment and reproductive maturity. Also, seed production of late seral species often exhibits periodicity or occurs only during favorable years (Oliver 1981). If a disturbance does not coincide with a high seed production year, late seral species may be slow to establish or may not establish on the site at all (Connell and Slatyer 1977). To insure the presence of late seral forest species in all of the forested biomes, it is usually necessary to seed, or more frequently, to transplant the desired species.

Deciduous Forest

In the deciduous forest, fire is a less significant cause of disturbance than in the coniferous forest, but minor fires may be relatively common under natural conditions. Trees often become senescent, die, and are blown down by wind (tip-ups). If trees fall individually, isolated gaps in the forest are created and a regeneration mosaic may develop. Vegetation regeneration can result from suppressed seedlings, root-sprouts, rhizomes, and other surviving vegetative structures in addition to seeds (Oliver 1981). In mature and old northern hardwood forests of the United States, many of the tree species are shade tolerant and can germinate and establish under a closed canopy (Canham 1989). The number of canopy trees growing in gaps as saplings can be high (37 to 67%) and may result in

significant regeneration of these sites (Lorimer et al. 1988). Seed production of late seral species may be highly variable among years and seeds of late seral species are often short lived. The composition of the seed bank in mature forests may be poorly correlated with that of the standing vegetation and seeds of early species may have the highest abundance (Pickett and McDonnell 1989). Microsite requirements for seedling establishment of late seral species can be highly specific (e.g., Borchett et al. 1989).

Plants with many different life history and physiological traits establish rapidly following disturbance. In many cases late seral dominants establish immediately following disturbance (Drury and Nisbet 1973; Christensen and Peet 1981). As succession proceeds, changes in both the physical and chemical environment occur that substantially influence competitive interactions and species replacement (Bormann and Likens 1979). Categories of shade tolerance have been developed for many deciduous tree species (Hicks and Chabot 1985). As in coniferous forest, species responses to shading may be determined in part by availability of other resources (Smith and Huston 1989).

Secondary succession in deciduous forest appears to have a deterministic component that is based on the life history traits of the available species and resource availability. A stochastic component reflects the site history and the characteristics of the disturbance (Halpern 1989; Houston and Smith 1987; Smith and Huston 1989). Initial colonizers may influence successional outcomes (Drury and Nisbet 1973; Connell and Slatyer 1977), but species composition often becomes more predictable as succession proceeds (Christensen and Peet 1984). Late seral stage dominants may be present from the beginning of the successional sere and apparent successional stages may be expressions of changing dominance due to differences in lifespans and environmental tolerances (Egler 1954). Regeneration series are often sufficiently predictable that they can be modeled using an individual-based approach that accounts for resource availability (e.g., JABOWA/FORET forest simulation models) (Botkins et al. 1972; Shugart 1984; Huston and Smith 1987). Development of the climax phase is often more rapid (200 to 500 years) than in all but the southern coniferous forests.

Reclamation of severely disturbed deciduous forests involves many of the same methods used in coniferous forests. A protective mulch may or may not be required depending upon the nature of disturbance and climate regime. It is usually necessary to provide seed or propagules of the mature forest species and to control competition. Post disturbance forest regeneration can result from suppressed seedlings, root-sprouts, rhizomes, and other surviving vegetative structures in addition to seeds (Oliver 1981). In the reclamation of severe disturbances in deciduous forest, topsoil can be used as a propagule source to significantly increase the diversity and productivity of early seral ecosystems (Wade 1989). The effectiveness of topsoil as a propagule source will be dependent upon the harshness of the site, the degree to which the topsoil has been degraded through past disturbance, and the current vegetation on the site from which the topsoil originates.

On reclaimed areas in deciduous and other forest biomes, vegetation structure can influence seed dispersal by both birds and mamnmals. Seeds of many species pass through the intestinal tracts of birds and are deposited in feces. The presence of vegetation of suitable height and size for perches, or even artifical perches, can serve as centers of invasion for many plant species (Hoppes 1988).

Boundary shape of disturbed lands and species composition of nearby undisturbed land can influence natural rates of species invasion and succession. Hardt and Forman (1989) found that stems of woody species extended farther into surface mines reclaimed with grass cover opposite concave than convex boundaries. A "concave-convex reversal" occurred a decade later when filled-in coves extended more rapidly toward uninvaded areas. Overall species composition within adjacent forest was a poor predictor of composition of the colonizing community. Abundance of animal-dispersed species was positively correlated with their abundance in adjacent undisturbed areas. No such relationship existed for wind-dispersed species.

Rain Forest

Mature rain forests are rarely subject to fire (Whitmore 1975) and drought and ice storms do not occur. Consequently, wind is the major agent of disturbance, acting either on individual trees or moderate-size groups of trees (tens to hundreds of hectares). In areas with steep topography, mass wasting may be important. Individual trees may persist for relatively long periods—100 to 1,000 years (Budowski 1970), with the accumulation of epiphytes increasing the probability of blow down (Strong 1977). Openings in the forest that result from tree blown down often form a mosaic of small patches that are characterized by varying moisture, temperature, and light regimes (Rickleffs 1977).

Rain forests exhibit a high degree of complexity and birds and mammals are usually more important dispersal agents than wind (Gentry 1982). Mammal and bird dispersal to a gap may increase over time as both shelter and food resources increase (Schupp et al. 1989). Ants may serve as important secondary dispersers (Roberts and Heithaus 1986). Seed longevity in tropical forests may be shorter than in more temperate areas due to the abundance of fungi, pathogens, and predators (Garwood 1989). Seedling mortality may also be high as a result of fungi, pathogens, and predators (Schupp et al. 1989). Germination and establishment occur rapidly following disturbance, but the majority of early colonizers that originate from seed are not those that are present in the mature forest (Farnworth and Golley 1974; Gomez-Pompa and Vazquez-Yanes 1981; Saulei and Swaine 1988). Regeneration also occurs from a variety of vegetative propagules and, depending upon the severity of disturbance, advance regeneration can be a significant factor in establishment (Uhl et al. 1988).

The vegetation not only alters the soil environment but also creates distinct temperature and light gradients that may extend dozens of meters into the canopy (Ricklefs 1977). Competition for water may occur in humid rain forests that have several consecutive months in which potential evaporation exceeds precipitation (Deshmukh 1986). More often competition is related to light or nutrients. Although the importance of light gradients and degree of shade tolerance in tropical forest regeneration is generally recognized, species responses to these gradients and consequent effects on successional patterns have been variously interpreted (Whitmore 1989a; Lieberman et al. 1989; Martinez-Ramos et al. 1989).

It has been estimated that 1 to 2% of the canopy areas is disturbed yearly through natural processes in both temperate and tropical forests. In tropical forests this appears to result in a high degree of spatial and temporal variability in the extent of canopy disturbance and, consequently, in light gradients (Lieberman et al. 1989), species composition and turnover, and population sizes (Whitmore 1989b). On severely disturbed sites (e.g., abandoned farms), succession may be retarded by the slow rate at which primary forest species become established (Uhl 1987). The time required to reach "climax" is relatively long (250 years or more) because the mature canopy species grow slowly (Richards 1952) and many environmental and floristic changes occur during succession.

Due to the high precipitation, severely disturbed sites in rain forests have a high potential for soil erosion. Thus, reclamation in rain forests requires extreme care to insure slope stability and to prevent the loss of soil and its nutrients. Reclamation of nutrient-poor ancient soils (primarily Oxisols) and of soils in which nutrients have been depleted through long-term cropping may require the addition of organic matter, nutrients, or both to reestablish forest vegetation (Deshmukh 1986). Artificial establishment of vegetation (seeding or transplanting) is seldom necessary because of the rapid natural recolonization of vegetation following disturbance (Hamilton 1990). Since late seral species may be slow to establish following severe disturbance, enrichment planting may be useful in some cases. However, the full complement of species can seldom be restored and, except on nutrient-poor soils, natural regrowth outcompetes planted trees.

Relationship of Reclamation Goals to Succession

There are three common goals of reclamation. All have a strong successional basis. Perhaps the most frequent goal of reclamation is to construct or reestablish an ecosystem that will structurally and functionally resemble the predisturbance native ecosystem (Allen 1988). When this is actually accomplished, it is most accurately termed restoration. A necessary assumption for restoration is that the predisturbance ecosystem is at or near climax and exhibits a high degree of stability.

A second possible goal of reclamation is to arrest succession at a low or intermediate seral stage. This may be desirable when the end land use is dependent upon species (plants or animals) that are abundant in the arrested seral stages. For example, in coniferous forests ungulate species such as elk and deer are often dependent upon early to mid-seral communities to provide the necessary habitat for their survival. If a reclamation goal were to increase or maintain deer and elk habitat, it would be desirable to promote establishment of shrubs or browse species but to delay establishment of late seral tree species for as long as possible.

A final goal may involve a totally different successional endpoint and, consequently, trajectory than that of the native undisturbed ecosystem. There are several instances in which this may be appropriate. The nature of the disturbance may place constraints on both the ability to reclaim a site and the subsequent successional processes that occur on that site. Reclamation of abandoned mine sites often involves substrates that differ significantly from those of the surrounding ecosystem and that may also contain toxic materials. It is often impossible and sometimes undesirable to establish the original native vegetation (due to plant uptake of heavy metals, etc.) on these sites without extensively ameliorating the substrates and topsoiling them. The reclamationist may have the opportunity to reclaim a site so that it will have a more desirable successional trajectory than the predisturbance ecosystem. This is often the case when surrounding areas have been previously seeded to monocultures or degraded due to overgrazing or other land uses. The reclamationist can improve the nutrient and water holding capacity of soils through proper soil handling and amelioration and can increase species diversity by direct replacement of topsoil and careful selection of seeding mixes.

Reclamation success is often evaluated by comparing the reclaimed area to a reference area or other standard chosen to represent the desired successional stage (Chambers and Brown 1983). The reference area is often part of an adjacent undisturbed native ecosystem. There are several potential problems with this approach. Comparisons of the reclaimed and reference area or standard are based on a relatively short time interval (usually 3 to 10 years) (see Surface Mining Control and Reclamation Act 1977). Consequently the stage of succession of the reclaimed and reference areas or standards may or may not be similar at the time of measurement or the successional trajectories may differ. Also, the attributes measured may not provide a good indication of the real successional trajectories.

The system attributes measured to evaluate reclamation success usually only include those related to vegetation structure such as number of trees and shrubs, percent cover or biomass of herbaceous species or species diversity (Chambers 1983; Chambers and Brown 1983). A necessary assumption is that if the vegetation structure of the reclaimed and reference area or standard are similar, the functional system attributes will also be similar. The practical reasons for this are that the time frame allotted for

determining reclamation success in short and that detailed measurements of many functional system attributes are much more expensive and difficult to obtain than measurements of structural system attributes. A serious omission in many current evaluations of reclamation success is the assessment of soil properties and of the soil biota (see M. Allen and Zak et al., this volume). In many cases, soil properties, including the soil biota, provide an excellent indication of the potential long-term vegetation productivity (Doll and Wallenhaupt 1985) and of successional trajectories (Biondini et al. 1985). Also, disturbance is an integral part of most natural ecosystems and a successfully reclaimed area should exhibit recovery rates and processes similar to the reference area. How a restored or reclaimed ecosystem reacts to normal disturbance (fire, grazing, tree blowdown, etc.) compared to the reference area ecosystem can be one criterion used to evaluate reclamation success.

Some potential successional trajectories of reclaimed and reference areas are illustrated in Figure 3. The y-axis reflects any attribute, abiotic or biotic, measured to evaluate reclamation success. The x-axis is the time interval required to obtain climax. The ideal situation is that over time the reclaimed area converges with the reference area (Fig. 3a). A less desirable outcome is that the reclaimed area diverges from the reference area (Fig. 3b). This may occur even if certain attributes of the reclaimed and reference areas are highly similar at the time or under the conditions that the attribute are measured. Another possibility is that the reclaimed area parallels the reference area without divergence or convergence (Fig. 3c). This may

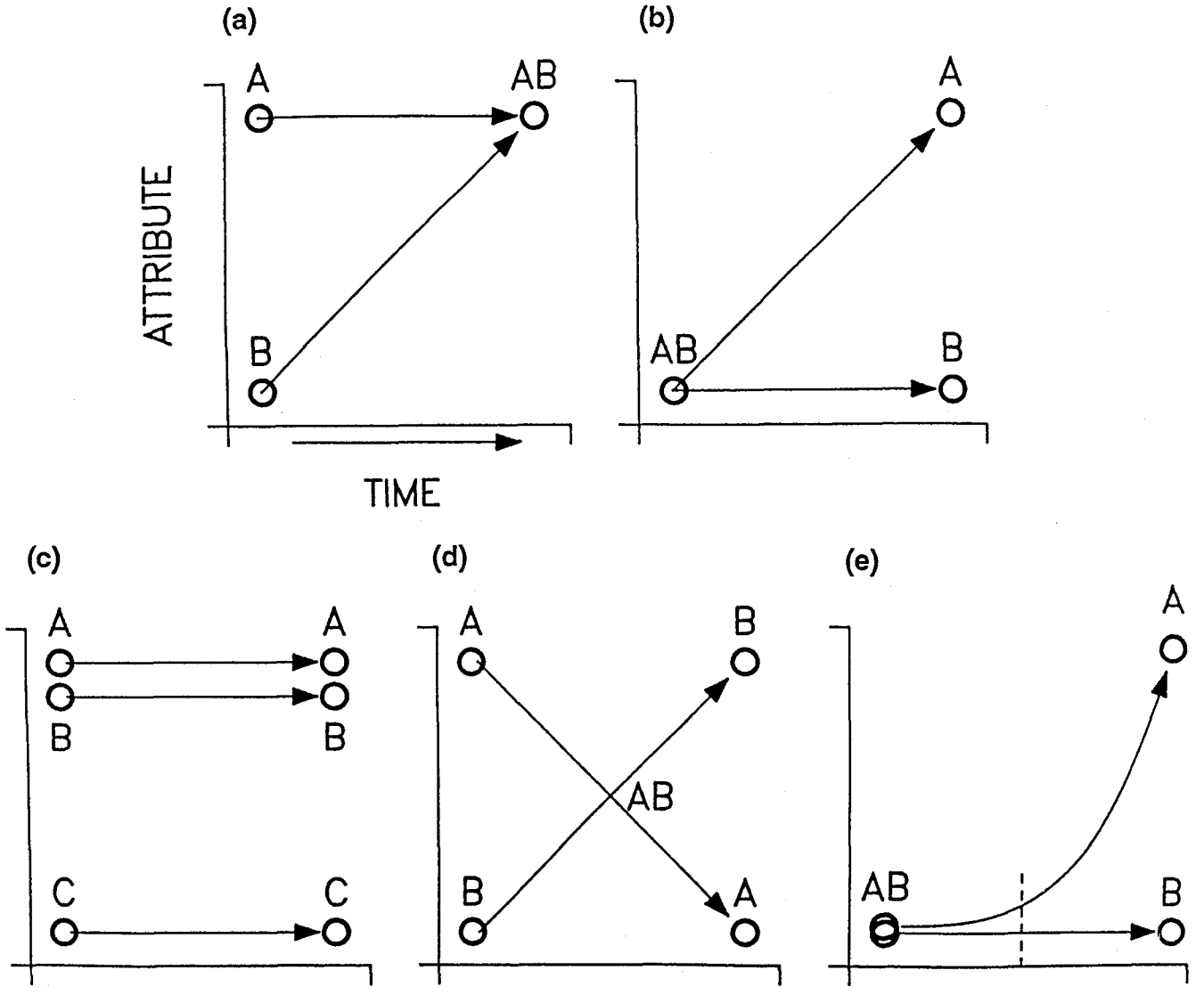

Figure 3.—Potential successional trajectories of reclaimed and reference areas. The y-axis represents any attribute measured to indicate the progress of succession or the success of reclamation. The x-axis is the time interval required to obtain climax. Different scenarios include: (a) the reclaimed area converges with the reference area; (b) the reclaimed area diverges from the reference area; (c) the reclaimed area parallels the reference area without divergence or convergence; (d) the reclaimed and reference areas may change in different directions (e.g., due to new or different types of management); and, (e) changes may exhibit various functions. The point in time when the attribute is measured affects perceived reclamation success.

be more or less desirable depending upon how similar the two areas were initially. Figures 3d and 3e illustrate the potential effects of land uses and management on comparisons of reference and reclaimed areas. The reference area may deteriorate during the reclamation period through disturbance associated with mining activities (Fig. 3d). In contrast, the successional trajectory of the reference area may change if it is released from land uses such as grazing through exclosure or some other form of protection (Fig. 3e). The point in time during which the measurements are made often determines the degree of perceived similarity and, consequently, reclamation success.

The same figure can be used to visualize the manner in which different ecosystem attributes change during succession. Attributes that exhibit little or no change or that vary randomly during succession are of little value in detecting successional trajectories. In some cases, it may be necessary to examine more than one attribute to ascertain real trajectories.

The effects of different successional starting points and trajectories on successional outcomes are related to a hypothetical reclamation effort in Figure 4. Arrows in the diagram represent successional trajectories. The original condition reflects the "normal" successional sere which may also be the reclamation goal. The reclaimed community may resemble either a successional or a climax-type community initially. If restored environmental conditions are similar to the original community and the proper species establish, a reclaimed early successional community may resemble the original successional community, or eventually, the climax community. If the reclaimed community is similar to a "normal" climax for the region in terms of both environmental conditions and species. It will undergo little change and the reclamation effort can be termed restoration. If environmental conditions or species are significantly different from the original conditions, reclaimed successional or climax-type communities may follow new trajectories toward new, possibly unique, climax-type communities. Some reclaimed successional communities may also go to arrested seral stages for significant periods of time.

Reclamation Goals and Success in Different Biomes

The successional processes that occur in the different biomes often dictate reclamation goals. Because of the differences among biomes in the length of time required to obtain climax, the degree to which reclamation success can be measured varies considerably.

Due to their extreme climatic regimes, desert and tundra ecosystems have often been cited as being among the most difficult biome types to reclaim following disturbance (Brown et al. 1978). They often exhibit variable temperature and precipitation regimes that result in a high degree of unpredictability (MacMahon 1981). Seed production is highly variable among years and plant establishment is frequently episodic. Despite these limitations, specific reclamation methodologies have been developed for both deserts and tundra that are highly effective (e.g., Aldon 1982; Brown et al. 1978; Brown and Chambers 1989). If the original soil conditions are restored, a carefully selected mixture of native species is seeded or transplanted, and the proper conditions for establishment are provided, the reclaimed ecosystem will rather quickly resemble the surrounding area. It may not be possible to establish the complete compliment of species immediately. In many desert and tundra ecosystems the predisturbance physiognomy can often be approximated through natural regeneration within 10 to 50 years. This timeframe can often be accelerated with proper reclamation methods.

For both deserts and tundra, often the only reclamation goal that makes ecological sense is the reestablishment of a native, late seral ecosystem. Native perennial species are the most stable component of these biomes and they should be used to evaluate reclamation success. Since dense stands of species with similar life forms and growth responses often retard colonization of other species (e.g., Brown et al. 1984), a variety of species with diverse life forms and growth responses should be present. Plant cover and production may be highly variable among years in deserts (West 1983). Also, since plant establishment is often episodic and plant growth can be slow in both deserts and tundra, it is necessary to monitor reclaimed areas for a reasonably long period to determine if reclamation success has been achieved.

In grassland and forest biomes, seed and other propagule availability is often high and, given the proper edaphic conditions, plant establishment can occur rapidly. For grasslands, the physiognomy of the site is often readily duplicated. Obtaining the desired species compliment and rare species is more difficult, especially if high densities of early seral, exotic, or introduced species occur on the site (Douglas 1965; Rice 1989). Reclamation goals may include restoration of a predisturbance or of a late seral type ecosystem if the predisturbance ecosystem is in an earlier seral stage. Native prairie restoration in the United States has been quite successful, but the cost is often high and other ecosystem components such as fire and herbivores must be carefully managed (Kline and Howell 1987). The ability to completely restore and manage these ecosystems will improve with increased research (Cottam 1987). Other reclamation goals for grasslands include successional trajectories that differ from the late seral condition. Arrested successions are seldom appropriate since they are often dominated by "undesirable" early seral species. Many former grasslands have been converted to pastures or croplands which are restored to the same end land use during reclamation.

Disturbances in forested biomes, especially those on mesic sites, are often considered the easiest to reclaim because of an abundance of propagules and rapid plant establishment. However, because of the nature of successional processes and the length of time required for

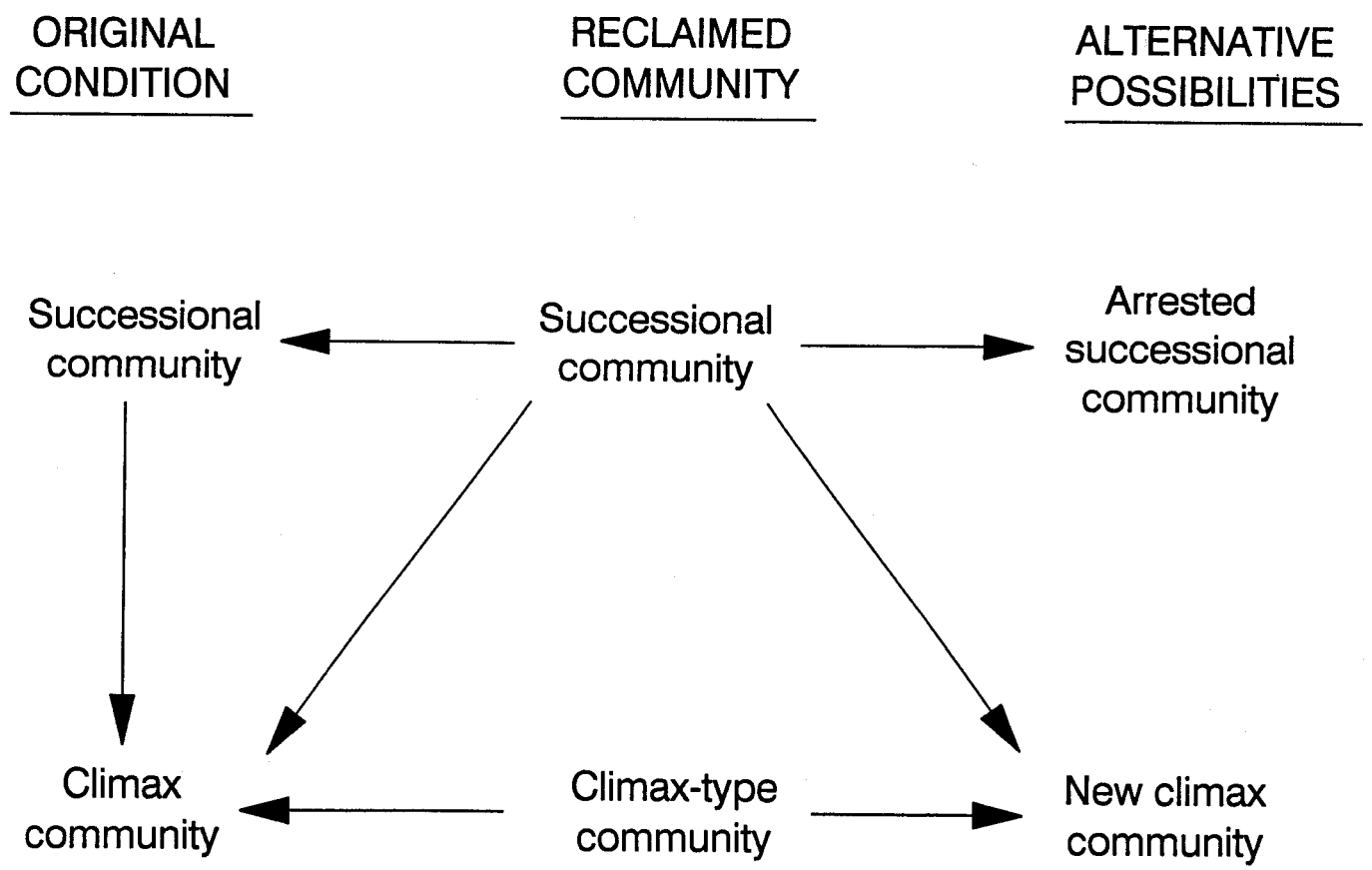

Figure 4.—Possible successional outcomes for a hypothetical reclamation effort. Initial reclamation may result in communities that resemble successional or climax-type communities. The reclaimed communities may eventually resemble the original communities or they may develop into new climax-type communities. Reclaimed early seral communities may remain unchanged as arrested successional communities.

succession in forests, it will almost never be possible to reclaim a forest so that it resembles a late successional stage within the bonding period. Late seral forest species are often difficult to establish, especially if propagules of early seral, exotic, or introduced species are already abundant on the site (Oliver 1981). Seed production of late seral forest species is often periodic and the seeds are often short lived. Since late seral forest species frequently exhibit slow growth rates and are slow to reach reproductive maturity, the physiognomic complexity of forests is slow to develop.

In forests, reclamation goals can include the establishment of early, mid- or late seral ecosystems representative of the predisturbance area or of ecosystems with totally different successional trajectories. Due to the length of time required for forests to reach late seral stages, reclamation success must necessarily be evaluated from early to mid-seral type ecosystems, regardless of the reclamation goal. Successional outcomes in forests may be highly dependent on the initial colonizers and are not always predictable (Drury and Nisbet 1973; Connell and Slatyer 1977). It has been suggested that species composition should become more predictable as succession proceeds and the influence of the pioneer community decreases (Christensen and Peet 1981, 1984). If the reclamation goal is to reestablish a particular mid- or late seral ecosystem, it will be necessary to insure that the dominant species for that particular seral stage have been established within the reclaimed area before bond release.

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