

EFFECTS OF ALIEN PLANTS ON NATIVE ECOSYSTEMS*

Peter M. Vitousek

ABSTRACT

Invasions by alien plants can change the large-scale functioning of native ecosystems and alter the population dynamics and community structure of native species. Such ecosystem-level changes affect the ways local systems interact with surrounding ecosystems, with downstream ecosystems and groundwater, and with the atmosphere. Large-scale changes in ecosystems caused by biological invasions represent a specific and convincing demonstration that the characteristics of individual species are important at the ecosystem level, and studies of biological invasions thus offer the possibility of integrating the approaches employed by physiological, population, community, and ecosystem-level ecology. The evidence that alien animals alter native ecosystems is strong, and such effects are widespread. A few examples of the effects of alien plants are equally strong, but much of the evidence for ecosystem-level effects of plants is anecdotal. Hard evidence for the system-level effects of biological invasions may help to build support for control of invasions, target resources to the most important species, and address concerns as far afield as the ecological consequences of releasing recombinant ("genetically engineered") organisms.

INTRODUCTION

Can alien plants alter the ecosystem-level properties of the areas they invade? Ecosystem-level properties include coarse-scale processes such as primary production, consumption, decomposition, water balance, nutrient cycling and loss, soil fertility, erosion, and disturbance frequency. Many of these properties are directly relevant to human health and well-being

*Based on a chapter by the author in *Biological invasions of North America and Hawaii*, ed. H.A. Mooney and J. Drake, 1986.

(Ehrlich and Mooney 1983), and their alteration can have significant consequences beyond the altered site (Bormann and Likens 1979).

Ecosystem-level characteristics are clearly influenced by the biota; in many cases they can fairly be regarded as wholly biotic properties. Nonetheless, it has been suggested that ecosystem-level properties are relatively little influenced by the identity or characteristics of any single species within an ecosystem (O'Neill *et al.* 1977). This point of view suggests that as long as some minimum diversity is present, most of the available resources will be fully utilized (Mooney and Gulmon 1983), and ecosystem characteristics will be independent of exactly which species are represented. This argument can be developed most easily for plants, because all plants require carbon dioxide, water, and the same mineral nutrients, and all these resources are obtained and used in similar ways. If this is true, then resource availability and environmental properties control both the biotic composition (Tilman 1982) and ecosystem-level properties (Rosenzweig 1968) of an area.

In contrast, a number of investigators have evaluated the significance of particular species or species groups in controlling ecosystem properties. The potential importance of understory trees as nutrient pumps (Thomas 1969); of early successional species in reducing run-off of surface water, erosion, and nutrient losses (Marks and Bormann 1972; Marks 1974; Foster *et al.* 1980; Boring *et al.* 1981); and of spring ephemeral species as "vernal dams" (Muller and Bormann 1976; Blank *et al.* 1980; Peterson and Rolfe 1982) has been suggested. Most of these studies demonstrated that a particular species takes up energy, nutrients, or water out of proportion to its biomass or apparent abundance in a community; but most studies to date have failed to show that ecosystem properties would be different in the absence of that species.

An examination of biological invasions of alien plants can provide unambiguous evidence for or against the ecosystem-level importance of individual species. We know that the characteristics of individual species are important on lower levels of ecological organization, and we know that biological invasions can alter native populations and communities (Elton 1958; Jarvis 1979; Clark *et al.* 1984). If biological invasions of alien species can alter ecosystem properties or processes, then the characteristics of individual species must be important on the ecosystem level as well.

There is substantial evidence that alien species can alter the characteristics of native ecosystems (Vitousek 1986). This evidence is much stronger for animal invaders than it is for plants (Singer *et al.* 1984; Stone and Scott 1985), in part because the effects of animals probably are greater than those of plants (on the average) (Vitousek 1986), and in part because too many studies of plants have been anecdotal rather than quantitative. Nonetheless, there is sufficient evidence suggesting that alien plants alter ecosystem properties. A systematic, quantitative study of the effects of alien plants is likely to prove rewarding, both practically and scientifically.

INVASIONS BY ALIEN PLANTS

Given the similarity in resource requirements among plants, it would seem that an alien that altered the properties of the natural ecosystem it invaded would have to either 1) gain access to resources at times that the natives are inactive or from locations that the natives cannot reach; or 2) be able to utilize those resources more efficiently than the natives. Different species of plants differ in resource use in a few striking and many subtle ways (Denslow 1980; Tilman 1982). For example, evergreens have access to light during "good" days within cold or dry seasons and therefore can obtain more energy than deciduous plants (Chabot and Hicks 1982). In contrast, deciduous plants may use water more efficiently than evergreens by dropping leaves during a dry season. One difficulty with studying the effects of invasions of alien plants is that many aliens tend to dominate disturbed sites (Allan 1936; Egler 1942; Smith 1985; Mooney and Drake 1986). It can, therefore, be difficult to separate the effects of alien species *per se* from the effects of the disturbance that allows them to establish. For example, Ewel (1986) showed that South Florida ecosystems dominated by the alien Brazilian peppertree, also known as Christmas berry (*Schinus terebinthifolius*), were very different from native ecosystems, but that an entirely novel anthropogenic disturbance (rock plowing) allowed *Schinus* to invade and succeed. Separating the effects of rock plowing and of Brazilian peppertree is difficult.

In this paper, I will concentrate on cases where aliens invade undisturbed native ecosystems, or where they clearly change the course of succession once they invade disturbed areas (Vitousek 1986). I will examine major ways in which plants can differ in resource acquisition or utilization, and cite examples in which biological invaders have been demonstrated to alter ecosystem properties because of differences in resource acquisition or use. I will then discuss interactions between alien plants and agents of disturbance such as fire and animals.

Differences in Life Form

In natural succession, increased productivity and nutrient use often occur when a new life form (e.g., perennial versus annual, shrub versus herb) is added (Odum 1960; Woodwell 1974). Perennials and woody plants can acquire more resources by maintaining a perennial root system that goes deeper into the soil, by maintaining evergreen leaves that are active year-round, or by regenerating deciduous leaves rapidly from storage (rather than *de novo* from current photosynthate). More efficient resource use could also result from the maintenance of internal storage pools of nutrients (Chapin 1980; Vitousek 1982; Fife and Nambiar 1984; Birk and Vitousek 1986).

It follows that alien plants could alter ecosystem properties when they add a life form that is not represented in the native flora. Perhaps the best example of this sort of change is provided by tamarisk or salt cedar (*Tamarix* spp.), a genus of riparian-zone invaders in the arid southwestern United States (Robinson 1969). Salt cedar requires wet areas for germination and early growth, but it is able to maintain itself on water from deep in the soil once it is established. Further, it has an

extraordinarily rapid rate of transpiration, which represents a significant pathway of water loss from reservoirs in the arid and semi-arid Southwest (Horton 1977). Salt cedar also invades natural springs and water courses in desert regions. For example, Eagle Borax Spring in Death Valley was invaded by salt cedar in the 1930s or 40s. By the late 1960s, rapid transpiration by salt cedar had caused the complete disappearance of surface water from what had been a large marsh (Neill 1983; P.G. Sanchez, pers. comm.). When managers removed salt cedar from the site, surface water reappeared, and Eagle Borax Spring and its associated flora and fauna recovered (Neill 1983). It would be difficult to picture a more convincing illustration of the potential for an alien plant to alter ecosystem properties.

Floating aquatic weeds represent another life form that can greatly alter ecosystem properties. The water fern *Salvinia molesta* is a morphologically diverse floating weed that has been widely introduced in tropical river systems; its effects have been thoroughly studied in Africa (Mitchell 1970 in Mitchell *et al.* 1980), India (*cf.* Thomas 1981) and Papua New Guinea (Mitchell *et al.* 1980). It was introduced to the Sepik River in Papua New Guinea in the early 1970s. Within ten years, it had measurably altered productivity in floodplain lakes, reduced yields from fisheries, and changed surface water chemistry (Mitchell *et al.* 1980). In Kerala, India, floating islands of *Salvinia* 3-10 ft (1-3 m) thick were reported (Thomas 1981); paddy cultivation was under way on one of them! Such alien aquatic weeds represent an economic problem in many areas, and their ecosystem-level effects have been studied more thoroughly than those of most terrestrial invaders.

A number of additional examples of invasions by new life forms have been documented, among them Brazilian peppertree and *Melaleuca quinquenervia* in the Everglades (Ewel *et al.* 1981; Ewel 1986; LaRosa *et al.*, this volume). *Melaleuca* in particular is able to invade otherwise unaltered stands of dwarf cypress (*Taxodium distichum*) and to alter ecosystem-level water balance in the process (Ewel 1986). Similarly, North American and other treeline species grow well above local treeline in New Zealand (Wardle 1971) and Hawai'i. Wherever biological invasions add a major new life form to an area, ecosystem-level changes can be anticipated.

Alien plants with life forms that differ from natives in subtler ways could also have ecosystem-level effects. A large number of researchers have evaluated the effects of forest plantations, often composed of alien pines, on productivity, nutrient cycling, and soil properties (Nihlgard 1972; Egunjobi and Onweluzo 1979; Perala and Alban 1982; Feller 1983/84). The establishment of forest plantations generally requires substantial human intervention, so studies in plantations cannot fairly represent the influence of an alien species under natural conditions. Nonetheless, large effects related to the biology of the planted species are often observed. Pine plantations generally yield less water to runoff than the broad-leaf forests they replace (Swank and Douglass 1974; Feller 1981); this effect is due more to increased interception and evaporation in the pine canopy than it is to a longer season for transpiration. Additionally, increased litter production and decreased litter decomposition can lead to the formation of

a massive forest floor (one with a thick organic layer) (Egunjobi and Onweluzo 1979).

I do not know if such effects can be documented outside of plantation conditions. Monterey pine (*Pinus radiata*) is spreading from plantation areas into adjacent dry sclerophyll forests in Australia, where it is outgrowing the native eucalypts by a wide margin (Burdon and Chilvers 1977; Chilvers and Burdon 1983).

Resource Acquisition and Utilization

One major way in which plants differ in resource requirements is the presence of nitrogen-fixing symbioses in a few groups of higher plants. An alien plant with the capacity to fix atmospheric nitrogen could clearly be at a competitive advantage when invading a nitrogen-limited community. More importantly, nitrogen fixed by the invader would ultimately (often rapidly) be released in the soil and become available to other organisms. Primary production in the majority of temperate, boreal, and montane tropical ecosystems is limited by nitrogen availability; fixation of nitrogen by alien plants can therefore increase soil fertility, the amount of nitrogen in circulation, and net primary productivity.

Nitrogen-fixing aliens occur in many regions, including *Ulex* and *Leucaena* on many Pacific islands (Allan 1936; Egler 1942), Scotch broom (*Cytisus scoparius*) in the Pacific Northwest, and *Casuarina* in Florida and Hawai'i. Most often, relatively little is known of the nitrogen status of the area invaded. An exception is the recent invasion by firetree (*Myrica faya*) in young volcanic regions of Hawaii Volcanoes National Park on the island of Hawai'i. The young ash deposits invaded are extremely nitrogen deficient (Balakrishnan and Mueller-Dombois 1983; Vitousek *et al.* 1983), and they contain no native symbiotic nitrogen fixers. Firetree can form nearly monospecific stands, and its actinorrhizal root nodules fix nitrogen rapidly (Vitousek *et al.* 1987). Its invasion clearly increases soil nitrogen availability in young sites, and this increased availability alters productivity, nutrient cycling, and possibly even the rate and direction of primary succession. Firetree adds three times more nitrogen to open-canopied 'ohi'a (*Metrosideros polymorpha*) forests than do all natural sources combined (Vitousek *et al.* 1987). (Natural sources include rainfall, native lichens with blue-green alga symbionts such as *Stereocaulon vulcani*, blue-green algae growing on the lava or in association with cryptogams, particularly liverworts, and bacteria associated with decaying wood.) Moreover, biological invasions by a wide variety of alien plant species in Hawai'i are most successful on more fertile sites (*cf.* Gerrish and Mueller-Dombois 1980), so the invasion of firetree may increase the probability of further invasions. A similar relationship between soil fertility and the success of alien species has been observed in Western Australia (Bridgewater and Backshall 1981).

Several other nitrogen-fixing aliens are established and aggressive in Hawai'i (Smith 1985), although except for *Casuarina* they rarely dominate early in primary succession. All these aliens might have the

potential to facilitate further invasions, and many would be worth intensive study.

Another way in which alien plants can alter soil characteristics is by concentrating salts. The ice plant *Mesembryanthemum crystallinum* is an aggressive invader in California (Vivrette and Muller 1977) and Australia (Kloot 1983). It usually requires human intervention to become established; it is most abundant in degraded pastures. Once established, it concentrates salt from throughout the rooting zone onto the soil surface, thereby altering soil physical and chemical properties and interfering with the growth of potential competitors.

It has been suggested that particular species could affect ecosystem properties by bringing nutrients to the surface from deep in the soil, thus serving as "nutrient pumps," which keep high levels of essential nutrients in circulation (Thomas 1969). I know of no direct evidence that alien plants have altered ecosystem properties in this way, but I also know of no serious attempts to look for such effects.

Photosynthetic Pathways

Three major photosynthetic pathways occur in higher plants. These are termed C_3 (the most common pathway), C_4 (tolerant of high temperatures and relatively water efficient), and CAM (a rather stable but extremely water-efficient pathway found in succulent plants). Alien plants with the C_4 and CAM photosynthetic pathways are highly aggressive invaders in many areas otherwise dominated by plants with the more common C_3 pathway (Rundel 1980). Many grasses (*Andropogon*, *Melinis*, *Pennisetum*, and many others) are successful alien C_4 species in Hawai'i, while the cactus *Opuntia* is a common CAM invader. Ecosystem-level effects of the alternative photosynthetic pathways are likely but not yet established.

Phenology

The effects of phenological differences between aliens and natives are somewhat better documented. For example, Mueller-Dombois (1973) described a situation in which an alien bunchgrass (*Andropogon*) in Hawai'i maintained its life cycle responses to photoperiodic cues from its range in the southeastern United States. Consequently, in Hawai'i it grows during the dry season and is inactive during the rainy season. Transpiration is much reduced with *Andropogon* relative to native rain forest, and boggy conditions develop in formerly mesic or dry situations (Mueller-Dombois 1973).

Successional Position

Invading plant species could also alter ecosystem properties if they differed from natives in their position in succession (cf. Pickett 1976). Individual species are most often argued to be important on the ecosystem level when they invade immediately after disturbance, grow rapidly, and take up nutrients that might otherwise be lost from the site as a whole (Marks and Bormann 1972; Foster *et al.* 1980; but see Vitousek 1986). The European alien plant wood groundsel (*Senecio sylvaticus*) apparently functions in this way in unburned clearcuts in the Oregon Cascades (Gholz *et al.* 1985), taking up a substantial fraction

of the nitrogen and phosphorus cycled by the intact 450-yr-old Douglas-fir forest within two to three years following clearcutting. It is tempting to speculate that *Senecio* has entered a hitherto unfilled niche in these forest ecosystems, but it must be remembered that it colonizes following a novel disturbance. The functional equivalent of unburned clearcuts (large-scale disturbances that remove the canopy over a wide area but leave the forest floor intact) were uncommon in the Pacific Northwest prior to widespread logging. It is interesting that a native species, fireweed (*Epilobium angustifolium*), colonizes after both wildfires and slash burning in the Oregon Cascades (Gholz *et al.* 1985).

Disturbance Frequency and Intensity

Alterations in disturbance regimes represent another possible way in which invasions by alien species could alter ecosystem-level properties. Any subsequent ecosystem-level changes would result not from differences in resource acquisition or the efficiency of resource utilization, but rather from interactions between alien plants and agents of disturbance such as fire, animals, or diseases.

Alterations in fire frequency as a result of biological invasions have been clearly identified, although detailed work on their consequences remains to be done. Smith (1985) identified eight species of alien weeds in Hawai'i as "fire-enhancers" -- species that increase the areal extent or intensity of fires in areas where they are established. The most spectacular example involved broomsedge (*Andropogon glomeratus*) and bush beardgrass (*Schizachyrium condensatum*), both of which form dense, nearly complete canopies in seasonally dry areas after the removal of feral goats (*Capra hircus*). (*Andropogon* also spread and intensified in the presence of goats to some degree (J.T. Tunison, pers. comm.)). The areal extent of fires increased 1,800-fold after goats were removed, and the alien bunchgrasses were able to reestablish on the burned sites better than natives. The native shrub *pūkiawe* (*Styphelia tameiameia*), which successfully withstood centuries of feral goat browsing, was rapidly reduced by the fires (Smith *et al.* 1980). Species that alter hydrologic cycles (e.g., the *Andropogon* species described by Mueller-Dombois 1973, above) could also alter disturbance frequency.

Animals are also agents of disturbance to vegetation as well as potential vectors for pollination and dispersal. Interactions between alien plants and alien animals can clearly cause ecosystem-level changes. Caldwell *et al.* (1981) demonstrated that *Agropyron desertorum*, an introduced bunchgrass in the Intermountain West, produces three to five times more tillers following clipping or defoliation than the otherwise very similar native bunchgrass *Agropyron spicatum*. Grazing pressure from cattle *Bos taurus* gives *Agropyron desertorum* part of its competitive advantage. In Hawai'i, Smith (1985) stated that feral pigs (*Sus scrofa*) and a number of the most important and aggressive weedy plants, including strawberry guava (*Psidium cattleianum*) and a number of passionflower (*Passiflora*) species, reinforce each other's ability to invade native ecosystems. Pigs consume and distribute seeds of the invaders, and they also disturb areas of soil and create excellent conditions for seed germination and seedling growth. Soil characteristics

and a community structure distinctly different from those in native forests can be maintained by this interaction.

Ecosystem-level effects of interactions between alien plants and pathogens are less well documented. Alien plants are known to have been involved in the spread of alien pathogens to native species (Gardner and Hodges 1983), but the consequences of such pathogens for native ecosystems have not been studied.

CONCLUSIONS

In general, the best-documented illustrations of the importance of invading plants in altering ecosystem properties involve effects on the hydrologic cycle, while effects on productivity or nutrient cycling are usually more speculative. Information on water yield from natural ecosystems has been collected much more precisely and over a longer period of time than information on most other ecosystem properties. Perhaps if information of similar quality were available for other properties, we could detect many more subtle but pervasive effects of biological invaders.

Studies of the ecosystem-level effects of biological invasions are likely to become more widespread and visible in the next few years. For example, the international Scientific Committee on Problems of the Environment (SCOPE) recently sponsored an international program to examine biological invasions. Moreover, biological invasions are being used as one of the very few sources of information that can help us to identify the consequences of releasing organisms with altered DNA ("genetic engineering") (Halvorson *et al.* 1985). Biological invasions by alien species are not identical to the sorts of environmental releases now planned, but they may represent a model for the consequences of releasing more highly modified organisms in the future. Hawai'i is a nearly ideal place to study the effects of biological invasions, and perhaps by studying those invasions that we cannot now control, we will be able to provide economic resources to Hawai'i and an additional impetus towards controlling alien plants in the future.



Literature Cited

- Allan, H.H. 1936. Indigene versus alien in the New Zealand plant world. *Ecology* 17:187-193.
- Balakrishnan, N., and D. Mueller-Dombois. 1983. Nutrient studies in relation to habitat types and canopy dieback in the montane rain forest ecosystem, island of Hawaii. *Pac. Sci.* 37:339-359.
- Birk, E.M., and P.M. Vitousek. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands on the Savannah River plant, South Carolina. *Ecology* 67:69-79.
- Blank, J.L., R.K. Olson, and P.M. Vitousek. 1980. Nutrient uptake by a diverse spring ephemeral community. *Oecologia* 47:96-98.
- Boring, L.R., C.D. Monk, and W.T. Swank. 1981. Early regeneration of a clearcut southern Appalachian forest. *Ecology* 62:1244-1253.
- Bormann, F.H., and G.E. Likens. 1979. *Pattern and process in a forested ecosystem*. New York: Springer-Verlag.
- Bridgewater, P.B., and D.J. Backshall. 1981. Dynamics of some Western Australian ligneous formations with special reference to the invasion of exotic species. *Vegetatio* 46:141-148.
- Burdon, J.J., and G.A. Chilvers. 1977. Preliminary studies on a native Australian eucalypt forest invaded by exotic pines. *Oecologia* 31:1-12.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowack, and R.S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Andropogon* bunchgrasses. *Oecologia* 50:14-24.
- Chabot, B.F., and D.J. Hicks. 1982. The ecology of leaf life spans. *Ann. Rev. Ecol. Syst.* 13:229-259.
- Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11:233-260.
- Chilvers, G.A., and J.J. Burdon. 1983. Further studies on a native Australian eucalypt forest invaded by exotic pines. *Oecologia* 59:239-245.
- Clark, B., J. Murray, and M.S. Johnson. 1984. The extinction of endemic species by a program of biological control. *Pac. Sci.* 38:97-104.
- Denslow, J.S. 1980. Gap partitioning among tropical forest trees. *Biotropica* 12 (Suppl.):47-55.
- Egler, F.E. 1942. Indigene versus alien in the development of arid Hawaiian vegetation. *Ecology* 23:14-23.

- Egunjobi, J.K., and B.S. Onweluzo. 1979. Litterfall, mineral turnover, and litter accumulation in *Pinus caribea* L. stands at Ibadan, Nigeria. *Biotropica* 11:251-255.
- Ehrlich, P.R., and H.A. Mooney. 1983. Extinction, substitution, and ecosystem services. *Bioscience* 33:248-253.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. London: Methuen and Co.
- Ewel, J.J. 1986. Invasibility: lessons from South Florida. In *Biological invasions of North America and Hawaii*, ed. H.A. Mooney and J. Drake, 214-230. New York: Springer-Verlag.
- Ewel, J.J., D. Ojima, and W. DeBusk. 1981. Ecology of a successful exotic tree in the Everglades. *Proc. 2nd Conf. Sci. Res. Natl. Parks* 8:419-422. Washington, D.C.
- Feller, M.C. 1981. Water balances in *Eucalyptus regnans*, *Eucalyptus obliqua*, and *Pinus radiata* ecosystems in Victoria. *Austr. For. Res.* 44:153-161.
- Feller, M.C. 1983/84. Effects of an exotic conifer (*Pinus radiata*) plantation on forest nutrient cycling in southeastern Australia. *For. Ecol. Manage.* 7:77-102.
- Fife, D.N., and E.K.S. Nambiar. 1984. Movement of nutrients in radiata pine needles in relation to the growth of shoots. *Ann. Bot.* 54:303-314.
- Foster, M.M., P.M. Vitousek, and P.A. Randolph. 1980. The effect of *Ambrosia artemisiifolia* on nutrient cycling in a first-year old-field. *Amer. Midl. Nat.* 103:106-113.
- Gardner, D.E., and C.S. Hodges. 1983. Leaf rust caused by *Kuehneola uridinis* on native and non-native *Rubus* species in Hawaii. *Plant Diseases*. 67:962-963.
- Gerrish, G., and D. Mueller-Dombois. 1980. Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawaiian Islands. *Phytocoenologia* 8(2):237-295.
- Gholz, H.L., G.M. Hawk, A. Campbell, K. Cromack, and A.T. Brown. 1985. Early vegetation recovery and element cycles on a clearcut watershed in western Oregon. *Can. J. For. Res.* 15:400-409.
- Halvorson, H.O., D. Pramer, and M. Rogul, eds. 1985. *Engineered organisms in the environment: scientific issues*. Washington, D.C.: Amer. Soc. Microbiol.
- Horton, J.S. 1977. The development and perpetuation of the permanent tamarisk type in the phreatophyte zone of the southwest. In *Importance, preservation, and management of riparian habitat: a symposium*, ed. R.R. Johnson and D.A. Jones, 124-127. U.S. For. Serv. Gen. Tech. Rep. RM-43. Washington, D.C.: US Dep. Agric.
- Jarvis, P.J. 1979. The ecology of plant and animal introductions. *Progr. Phys. Geogr.* 3:187-214.

- Kloot, P.M. 1983. The role of common iceplant (*Mesembryanthemum crystallinum*) in the deterioration of medic pastures. *Austr. J. Ecol.* 8:301-306.
- LaRosa, A.M., R.F. Doren, and L. Gunderson. [this volume] Alien plant management in Everglades National Park: an historical perspective.
- Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* 44:73-88.
- Marks, P.L., and F.H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. *Science* 176:914-915.
- Mitchell, D.S. 1970. Autecological studies of *Salvinia auriculata* Aubl. Ph.D. thesis, Univ. London, London.
- Mitchell, D.S., T. Petr, and A.B. Viner. 1980. The water-fern *Salvinia molesta* in the Sepik River, Papua New Guinea. *Environ. Conserv.* 7:115-122.
- Mooney, H.A., and J. Drake, eds. 1986. *Biological invasions of North America and Hawaii*. New York: Springer-Verlag.
- Mooney, H.A., and S.L. Gulmon. 1983. The determinants of plant productivity -- natural versus man-modified communities. In *Disturbance and ecosystems: components of response*, ed. H.A. Mooney and M. Godron, 146-158. Berlin: Springer-Verlag.
- Mueller-Dombois, D. 1973. A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. *Trop. Ecol.* 14:1-18.
- Muller, R.N., and F.H. Bormann. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. *Science* 193:1126-1128.
- Neill, W.M. 1983. The tamarisk invasion of desert riparian areas. *Educ. Bull.* 83-4, Desert Protect. Coun., Spring Valley, Calif.
- Nihlgard, B. 1972. Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. *Oikos* 23:69-81.
- Odum, E.P. 1960. Organic production and turnover in old field succession. *Ecology* 41:34-49.
- O'Neill, R.V., B.S. Ausmus, D.R. Jackson, R.I. van Hook, P. van Voris, C. Washburne, and A.P. Watson. 1977. Monitoring terrestrial ecosystems by analysis of nutrient export. *Water Air Soil Pollut.* 8:271-277.
- Perala, D.A., and D.H. Alban. 1982. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. *Plant and Soil* 64:177-192.
- Peterson, D.L., and G.L. Rolfe. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *Amer. Midl. Nat.* 107:325-339.

- Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. *Amer. Nat.* 110:107-119.
- Robinson, T.W. 1969. Introduction, spread, and areal extent of saltcedar (*Tamarix*) in the western states. U.S. Geol. Surv. Prof. Pap. 491-A.
- Rosenzweig, M.L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. *Amer. Nat.* 102:67-74.
- Rundel, P.W. 1980. The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. *Oecologia* 45:354-359.
- Singer, F.J., W.T. Swank, and E.E.C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. *J. Wildl. Manage.* 48:464-473.
- Smith, C.W. 1985. Impact of alien plants on Hawai'i's native biota. In *Hawai'i's terrestrial ecosystems: preservation and management*, ed. C.P. Stone and J.M. Scott, 180-250. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.
- Smith, C.W., T. Parman, and K. Wampler. 1980. Impact of fire in a tropical submontane seasonal forest. *Proc. 2nd Conf. Sci. Res. Natl. Parks*, Vol. 10, *Fire ecology*, 313-324. San Francisco, Nov. 26-30, 1979. Natl. Park Serv.
- Stone, C.P., and J.M. Scott, eds. 1985. *Hawai'i's terrestrial ecosystems: preservation and management*. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit. Honolulu: Univ. Hawaii Pr.
- Swank, W.T., and J.E. Douglass. 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science* 185:857-859.
- Thomas, K.J. 1981. The role of aquatic weeds in changing the pattern of ecosystems in Kerala. *Environ. Conserv.* 8:63-66.
- Thomas, W.A. 1969. Accumulation and cycling of calcium by dogwood trees. *Ecol. Monogr.* 39:101-120.
- Tilman, D. 1982. *Resource competition and community structure*. New Jersey: Princeton Univ. Pr.
- Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *Amer. Nat.* 119:553-572.
- Vitousek, P.M. 1986. Biological invasions and ecosystem processes: can species make a difference? In *Biological invasions of North America and Hawaii*, ed. H.A. Mooney and J. Drake, 163-176. New York: Springer-Verlag.
- Vitousek, P.M., K. van Cleve, N. Balakrishnan, and D. Mueller-Dombois. 1983. Soil development and nitrogen turnover in montane rainforest soils on Hawaii. *Biotropica* 15:268-274.
- Vitousek, P.M., L.R. Walker, L.D. Whiteaker, D. Mueller-Dombois, and P.A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802-804.

Vivrette, N.J., and C.H. Muller. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecol. Monogr.* 47:301-318.

Wardle, P. 1971. An explanation for alpine timberline. *New Zealand J. Bot.* 9:371-402.

Woodwell, G.M. 1974. Success, succession, and Adam Smith. *Bioscience* 24:81-87.

