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STAND DEMOGRAPHY AND VEGETATION CHANGE[1]

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Abstract. Demography, the study of vital statistics, when applied at the stand-level of community organization, can contribute significantly to the predictability of vegetation change. This is particularly so in low-diversity biomes in which a few key species dominate the vegetation. Examples are presented from low-diversity forest biomes in the Pacific area, where degenerating and regenerating populations of major tree species are the principal determinants of vegetation change.

Introduction

Demography, the study of vital statistics, applied at the stand-level of community organization, relates to the history of a given stand of plants or vegetation in the field. Demography is a population concept, which has not yet become fully integrated into the concepts of vegetation science, but a stand of vegetation or a community is composed of populations. In low-diversity biomes, in which only a few canopy species dominate the vegetation cover, these dominants often exert a key role in the dynamics of such ecosystems. Under these conditions, population and community dynamics are almost synonymous or at least closely related. In other words, the demography of the dominant species may closely affect the rest of the community in spite of the fact that the other species of the community respond individually according to their own ecological adaptations.

In this paper, I will present a few researched examples from Pacific forest biomes, where events in stand demography relating in their simplest terms to the establishment, growth, development, and degeneration of cohort stands, are seen as playing a key role in vegetation change, thereby making the latter more predictable.

The Shimagare Phenomenon in Japan

In the central mountain range on Honshu Island of Japan, the subalpine fir forest is composed of two dominant tree species, *Abies veitchii* and *A. mariesii*. On the Pacific side of this mountain range, a peculiar pattern of dead stripes of trees, Shimagare in Japanese, is evident in several mountain locations, mostly between 2100 and 2600 m elevation. The phenomenon has attracted the attention of Japanese foresters, pathologists, geographers, ecologists, and physiologists for more than forty years (Kohyama 1984, 1988). It is now recognized generally as a stand-demographic phenomenon and can be explained as follows:

Northwestern Pacific typhoons cause occasional catastrophic blow-downs in these forests in form of striped patterns. These openings become filled with regeneration of the same two species. Reestablishment is more or less synchronous resulting in even-aged cohort stands. The cohort stands develop normally to maturity by undergoing self-thinning. However, intraspecific competition continues into maturity. The trees then become physiologically more uniform and stress one-another reciprocally. Trees at the wind-exposed side of the cohort stand are additionally stressed by harsh winds causing winter desiccation and then start to die from the two-fold stress, *i.e.* intraspecific competition surmounted by the harsh edge environment. Mortality begins at the stand edge and then proceeds domino-style inward, while at the same time new regeneration of the same species thrives under the dying trees. The mortality progresses at a rate of approximately 1m/year and occurs at an approximate stand age of 100 years.

The Shimagare phenomenon is almost identical to the fir-wave regeneration phenomenon in *Abies balsamea* forests studied first by Sprugel (1976) in the Adirondak Mountains of New York State.

The *Scalesia* Forest Dieback in the Galápagos Islands

Scalesia pedunculata is the dominant forest forming tree in the moist zone at middle elevations on Santa Cruz Island in the Galápagos. It is a member of a highly speciated endemic genus and grows very fast like a tropical weed tree (*e.g.* 2-3 m in height/yr). Recently, two publications have focussed on the mass dieback and regeneration phenomenon of this forest (Lawesson 1988, Itow and Mueller-Dombois 1988). Lawesson (1988) has documented four recurring mass diebacks and regenerations that occurred in the same biome as seen

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in Table 1.

Table 1. Four *Scalesia* dieback/regeneration periods in the moist zone of Santa Cruz*

Dieback/Regen.	Interval	El Niño yrs
1942	15 yr	1940
1957	14 yr	1956
1971		weak
1986	15 yr	1982/83

* adapted from Lawesson (1988)

There appears to be an interaction with strong El Niño years when very heavy rainfall occurs in the Galápagos Islands. However, El Nino occurs every year around christmas time and the principal predisposing cause of mass dieback seems to be the simplified cohort structure of the *Scalesia* forest which becomes destabilized when the cohort stands reach the senescing life stage following peak maturity. Hamann's (1979) permanent plot studies clearly show that *Scalesia pedunculata* is a short-lived perennial tree with a life span of only 10-20 years. Lawesson (1988) points out that fire during drought after certain dieback events may synchronize reestablishment of *Scalesia* cohorts over larger areas. Thus here, as in the Shimagare phenomenon, stand-level dieback and regeneration is a demographic event that interacts with two kinds of disturbances. First comes an occasional stochastic catastrophic disturbance that provides open areas for the invasion of an opportunistic species. The established cohort stand then becomes exposed to periodically recurring non-catastrophic physiological shocks (secondary disturbances) that trigger a stand into dieback once it has entered a demographically weakened life-stage. This in turn causes reitterations of the regeneration/degeneration cycle. The trigger factor, whose true nature is typically elusive in dieback forests, then becomes deterministic through an understanding of stand demography.

The *Metrosideros* Dieback in Hawaii

Another example of mass tree mortality is the *Metrosideros polymorpha* dieback in the Hawaiian rainforest biome which has been thoroughly researched since the early 1970's. Initially it was predicted by forersters to be a new alien disease (Petteys *et al.* 1975). When the disease hypothesis became untenable (Papp *et al.* 1979), abiotic environmental stress was implied as the principal cause (Hodges *et al.* 1986). However, no obvious environmental stress could be detected.

By comparing the Hawaiian dieback to other Pacific forests with dieback phenomena, notably the *Nothofagus* and *Metrosideros* diebacks in New Zealand, it became apparent that certain low-diversity forests comprise mosaics of cohort stands (Mueller-Dombois 1983). The mosaic segments in these forest biomes display their own demographically determined dynamics, similarly as do the individual plantation stands in the checkerboard pattern of a larger plantation system. In such commercial systems, however, cohort stands are usually harvested before they degenerate.

In natural forest biomes the causes of dieback have been explained by the cohort senescence theory (Mueller-Dombois 1983, 1986, 1988). The theory involves four factors, and time, as follows:

s = simplified stand structure in form of cohorts or even-aged stands
e = edaphically extreme habitats or those to which the colonizing species is evolutionary poorly adapted
p = periodically recurring physiological shocks in form of widely fluctuating habitat factors as caused by extreme weather events
b = biotic agents, which provide for the *coup de grace*
t = time in the sense of generation time or longevity, which is species-specific but usually shorter than the tree's life span attainable under optimum conditions

These factors are suggested to operate in a three-stage chain reaction as proposed by Sinclair (1967) for his decline disease theory, *i.e.*

(1) predisposing factors **(s, e, p)**
(2) inciting factor (**p** again)
(3) accelerating factor **(b)**

The species-specific stand-generation time **(t)** provides for the overriding time dimension relating to the different life-stages of a forest stand (i.e. regenerative/juvenile, pre-mature, mature, and terminal or breakdown stage).

Conclusions

The cohort senescence theory fits the three examples given here. It also can be used to elucidate the anthropogenically influenced forest decline currently of great concern in Central Europe and Eastern Australia (Mueller-Dombois 1990). As an ecological explanation, the cohort senescence theory changes our way of thinking about forest decline as a predominantly pathological problem. Apart from transcending disciplinary barriers, the cohort senescence theory also integrates plant demography with vegetation science, and physiological ecology with ecosystem and landscape ecology. In terms of vegetation change it provides a key to greater predictability when applied in the broader context of a biome.

For example, in the Hawaiian rainforest biome, the spatial configuration of dieback appears to be related to the spatial configuration of initial catastrophic disturbances and the subsequent colonization pattern of *Metrosideros* seedling cohorts. Moreover, three dieback/regeneration types have been distinguished, called replacement, displacement, and stand-reduction dieback. The first occurs on poor (oligotrophic) soil substrates on which *Metrosideros* saplings encounter reduced competition from other species. Displacement dieback implies successional displacement by other species in the recovery process. Under natural conditions these are tree ferns (*Cibotium* spp.) which are aggressive on nutrient-rich (eutrophic) soils. A new form of displacement dieback occurs through alien species invasion in certain segments of the wide habitat spectrum occupied by *Metrosideros polymorpha*. The third type, stand-reduction dieback, occurs where soil aging has progressed to an unfavorable nutrient and soil water status so that the recovering *Metrosideros* cohorts become dwarfed and fragmented.

The three dieback/recovery types are found in similar or modified form in the previously discussed forest biomes and all three have a stand-demographic basis.

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