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Relative abundance in an alien weed flora*

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Summary. Both relative abundance and absolute abundance of alien weed species in a large geographic region increased from the year 1900 to 1980. The increase in relative abundance may have been due to competitive displacement among the weeds, patterns of landscape disturbance, or simply time. The increase in absolute abundance indicates the ineffectiveness of past weed control policies in stemming weed migration. Combined, the two scales of alien weed abundance suggest that in the future we can expect an increasing diversity of increasingly common weeds.

Introduction

Weeds native to Africa and Eurasia are presently familiar sights in Australia and the Americas. Several species of these weeds spread rapidly after their initial introductions, but just as many, if not more, have remained in restricted locales. For example, of the three species of *Echium* that occur in Australia, *E. italicum* and *E. vulgare* have spread little and may have reached their distributional limits, whilst *E. plantagineum* has spread and still is spreading widely and rapidly (Fig. 1).

When organisms "invade" a new habitat, e.g. an abandoned agricultural field, a series of ecological interactions commence so that particular patterns of species' abundances are established. These patterns change with time until, presumably, a final and stable pattern is attained (see Fig. 3 in Whittaker 1972). Introduction of alien weeds into a large geographic region is not akin to invasion of adjacent taxa into abandoned fields, but nevertheless, analogous abundance patterns for a regional alien weed flora might occur and change as time progresses. In this report we (1) examine historical changes in abundance patterns of alien weeds in the northwestern USA, (2) hypothesize reasons for such changes, and (3) suggest implications of these changes for the future.

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For the purposes of this report we define an alien weed as any plant species that (1) exists without purposeful cultivation in regions wherein it did not occur prior to settlement of foreign peoples, and (2) tends to have a negative economic impact, no matter how obscure, in the region of concern

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Background

The states of Idaho, Montana, Oregon, Washington and Wyoming came under extensive and permanent influence of eastern American and Eurasian settlers mostly after 1850. Settlers brought with them, usually inadvertently, weeds of their homelands. Coinciding with the influx of early, primarily agricultural settlers and their weeds were a number of plant enthusiasts (agronomists, botanists, naturalists etc.). Fortunately, several land grant colleges and their associated herbaria were also established in the region in the latter decades of the 19th Century. Initial introduction and subsequent spread of many plants, therefore, were documented by preserved, labeled, herbarium specimens. We have evidence (unpublished data) that early plant collectors were efficient at establishing distributions of native weeds early in the collection history of the Northwest, and likewise were quick to collect new populations of spreading alien plants. As the number of residents, their mobility, and landscape disturbance increased in the five northwestern states, so too did the number and spread of alien weeds and the number of plant enthusiasts collecting those weeds. Thus in the Northwest plants have been collected continuously from the late 1800's to the present. The assembly of northwestern herbaria thereby represent a vast catalog of the introduction (~colonization), spread (~migration) and distribution (~commonness or abundance, cf. Hanski 1982) of all the introduced plants known for the region.

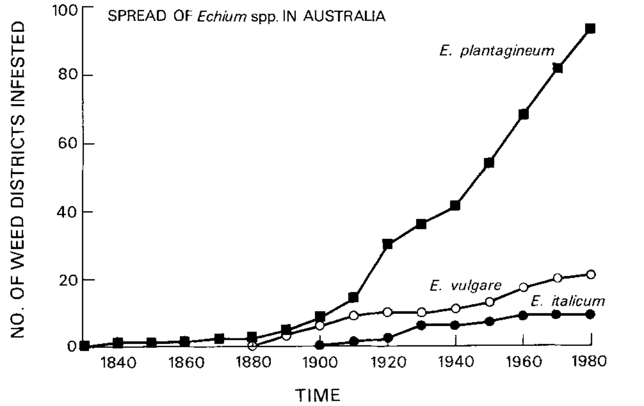

Fig. 1. Spread of *Echium italicum*, *E. plantagineum* and *E. vulgare* in Australia. Distribution data adapted from Piggin (1977), weed districts equivalent to latilongs (1° × 1.5°) used by the Australian Gazetteer

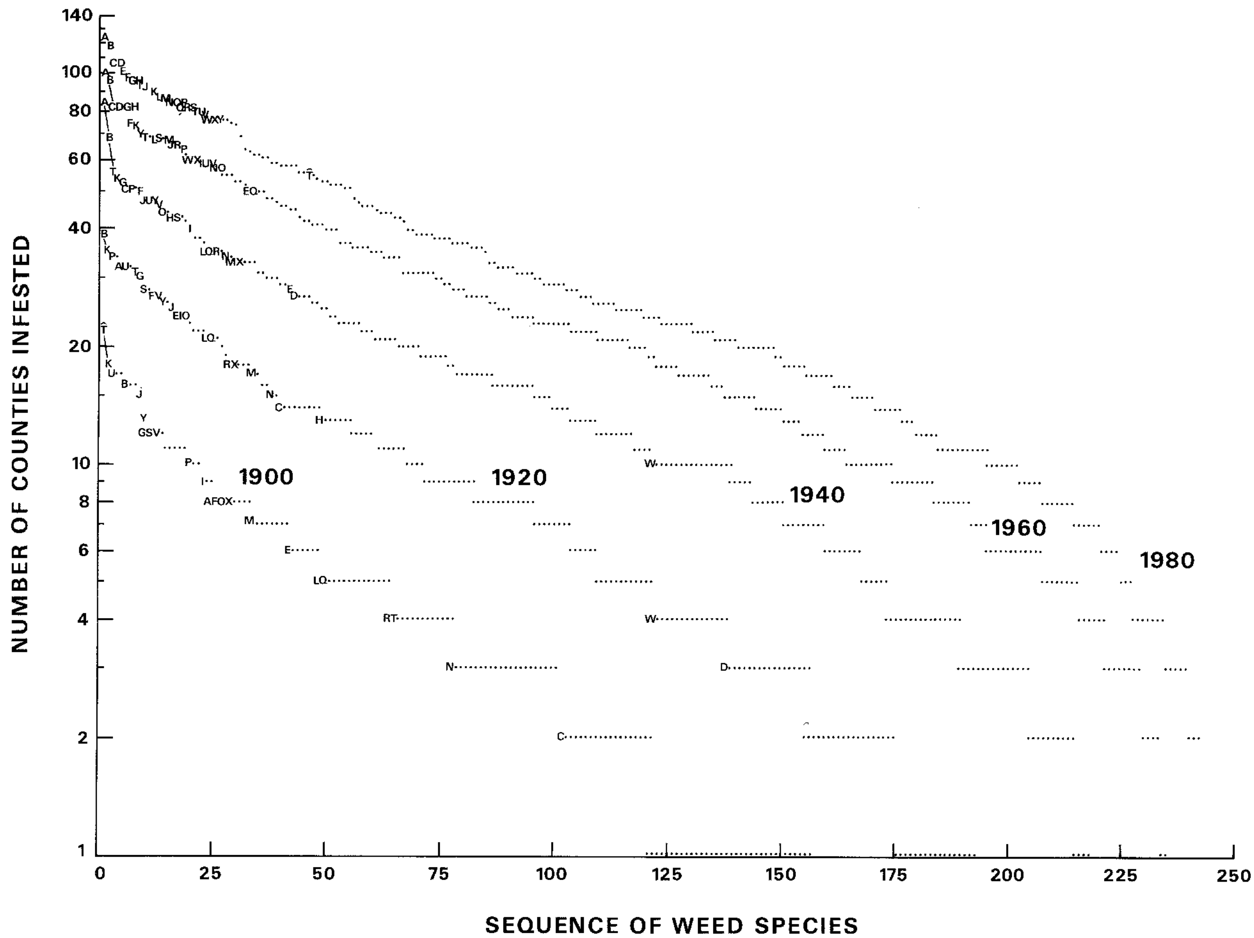

Fig. 2. Relative abundance (i.e. number of counties infested) of alien weed species in northwestern USA in 1900, 1920, 1940, 1960 and 1980. Ten species occurring in only one or two counties in 1980 have been deleted from the graph. Species A-Y are as follows: *Bromus tectorum A, Hordeum jubatum B, Thlaspi arvense C, Tragopogon dubius D, Cirsium arvense E, Sisymbrium altissimum F, Rumex acetosella G, Lepidium perfoliatum H, Convolvulus arvensis I, Salsola kali J, Plantago major K, Medicago lupulina L, Camelina microcarpa M, Descurainia sophia N, Taraxacum officinale O, Capsella bursa-pastoris P, Agropyron repens Q, Rumex crispus R, Lactuca serriola S, Erodium cicutarium T, Xanthium strumarium U, Polygonum convolvulus V, Bromus japonicus W, Setaria viridis X,* and *Vaccaria segetalis Y.* Note that species *D, H* and *W* were not present in 1900. (*Avena fatua*, an important weed in the northwestern USA, has not been included in the above analysis.) Nomenclature follows that of Hitchcock and Cronquist (1973)

Methods

From several regional Floras (Booth 1950; Booth and Wright 1966; Dorn 1977; Davis 1950; Hitchcock and Cronquist 1973; Moss 1959; Van Bruggen 1976) we recorded 250 non-native taxa currently in or with the potential to invade any of the five northwestern states; with a few exceptions these were nearly all Eurasian taxa. Species on this list were then examined for first-collection-by-county data in the following herbaria: ID, IDS, MONT, MONTU, RM and WSP. We supplemented herbarium-derived data with species locations from literature sources (e.g. Blankenship 1901) when available as well as our own field notes, but information of this type constituted $<5\%$ of the total data.

For each taxon the cumulative number of new counties in which it was found was calculated for each decade of the past century (ca. 1881–1980). These sums were equated with abundance in the same sense as "frequency" is used in Plant Ecology (e.g. Kershaw 1973). Taxa were then ordered as to their abundance on semi-log paper for each decade, which resulted in 10 dominance-diversity curves (*sensu* Whittaker 1975).

Although density and/or coverage are much better estimates of abundance than is frequency, such data are not available for any weed species over the range of its distribution in northwestern USA. Moreover, Hanski (1982) has found that geographic range is correlated positively with local density in both plants and animals; this provides additional justification for our use of frequency data.

Results

Dominance-diversity curves for the Northwestern alien weed flora in 1900, 1920, 1940, 1960 and 1980 are shown in Fig. 2. Shapes of the curves change with time, from a steeply sloping, nearly log-linear curve in 1900 to distinct skewness in 1980. Thus the abundance of alien weeds progresses through time, initially in a pattern with few dominant and many rare species, through log-normal distributions, to a highly skewed distribution in which occur several more-or-less equally common species and relatively few abundant or rare taxa. Changes in the concentration of abundance through time also is apparent from the decrease in Simpson's diversity index ($C = \Sigma P_i^2$, where P is the proportion of total abundance possessed by species *i*) with time: 0.0113, 0.0096, 0.0077, 0.0071 and 0.0058 for 20-year intervals from 1900–1980. The decrease is linear and statistically significant ($r^2 = 0.98$ $P < 0.01$) and conforms to the following equation: $C = -0.0000675$ (date) $+ 0.13925$. Extrapolating to the year 2000, concentration of dominance would be about 0.0043. Corresponding to this would be approximately 275 alien weed species with the most abundant taxon occurring in about 165 counties.

Not only do abundance patterns change with time, but the order of positions of each species in the patterns changes as well. The 25 most common weeds in 1980 are denoted by the letters A through Y in Fig. 2. Regressing back through time, these 25 species do not remain the most abundant weeds. In fact, three taxa, *Tragopogon dubius* (D), *Lepidium perfoliatum* (H), and *Bromus japonicus* either were not known or were very rare in the Northwest prior to about 1910. There was, initially at least, constant shuffling of weeds into and out of the top 25 species' positions.

Discussion

Any one interpretation of these results would be equivocal. Nevertheless, it may be useful to discuss them.

Time for dispersal. By 1890–1900 the basic railroad network that services the Northwest had been established (Mack 1981). Therefore, the potential for widespread and rapid dissemination of weed propagules existed. However, despite this, most alien weeds were not extensive at that time; abundance was concentrated in a few species. With varying rates of potential dissemination for each taxon, some species forged ahead and surpassed others until they reached their distributional limits. With time, slower moving species eventually increased to fill their potential geographic ranges. Thus only time might be required to produce the relative abundance curve characteristic of 1980.

Disturbance. Weeds are not characteristic of undisturbed landscapes. It is usually where humans have directly or indirectly altered natural landscapes that alien weeds proliferate (Salisbury 1961). With alien weeds so intimately tied to land use, perhaps changing patterns in relative abundance of alien weeds may be explained by changing patterns of disturbance. Roadsides are often conducive to weed growth (Frenkel 1970; Forcella and Harvey 1983) and probably weed migration as well. Thus we may use road construction and road use as examples of disturbance that are related to weed proliferation. Frenkel (1970) supplied data for the cumulative length of rural roads in California along with the number of registered motor vehicles from 1904 through 1960. Both data sets follow exponential curves over time, with lag periods terminating in the 1920's. Although rates of road construction and motor vehicle registration vary somewhat according to periods of economic depression and war, after 1920 both factors accelerated geometrically. They remained in these geometric phases at least until 1960. We suspect that the likely disturbances caused by roads and motor vehicles in California are an index of Man's total environmental alteration in the Northwest in the sense of timing and rate of occurrence. If so, then the total area suitable for alien weed growth in the Northwest at the turn of the century would have been an exponentially smaller fraction of what it was in 1980 as well as being much less diverse. Such a situation would have restricted the distribution of most alien weeds, whilst allowing a few particularly well adapted weeds to be especially common. As the extent and diversity of landscape disturbance increased along with associated niches and niche availability, so too could the number and relative abundance of most weed species.

Competition. Changing patterns of abundance in an alien weed flora correspond with expected diversity patterns along gradients of environmental rigour as well as successional community gradients (Whittaker 1972). In both of these cases interactions among species have been cited as causes for changes in relative abundance (MacArthur 1960, May 1975, Whittaker 1972). Mack (1981) has chronicled in detail the introduction, spread and competitive abilities of *Bromus tectorum* in the Northwest. He concluded that this weed may have attained its present status as the most abundant weed in the region (Figure 2) at least in part by competitive displacement of other weed species. Such an assertion is impossible to prove, but nevertheless, warrants consideration and may have bearing on relative abundance patterns. With a broad outlook in mind large geographical regions might be considered as communities exhibiting extraordinary numbers of niches and taxa. Arguments of homogeneity verses heterogeneity for communities are, of course, simply a matter of perspective; clearly, bay-breasted and myrtle warblers (*sensu* MacArthur 1957) would take issue with any ecologist who construed their spruce forest or tree to be homogeneous. In this sense then, patterns of abundance within regional floras may be indicative of niche allocation through competitive displacement not especially different from that which some think occur in communities, i.e. changing with time from patterns of niche pre-emption, to multiple niche boundaries, to random niche boundaries (Whittaker 1975).

Reasons for changing patterns of relative abundance of alien weeds notwithstanding, two aspects of these patterns, as shown in Figure 2, have important implications for the future. First, as time progresses the relative abundance of more and more weeds increases. We can expect, therefore, greater diversity of our major agricultural weeds in the future. Second, the absolute abundance of these same weeds also is increasing steadily with time despite our longstanding weed control efforts. This would seem to suggest that past weed control policies and practices have had little effect in abating weed migrations in the Northwest, and that radical departures from past norms may be required to stem the flow of weeds in the future.

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