WEEDS, INVADERS, AND COLONIZERS: WHO IS WHO AND WHY

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RESUMEN: Las malas hierbas, invasores y colonizadores son tres conceptos estrechamente relacionados, aunque no idénticos, que reflejan tres puntos de vista diferentes: antropocéntrico (las malas hierbas interfieren en los objetivos de gestión de los pueblos), ecológico (los colonizadores aparecen pronto en series sucesorias), y biogeográfico (las especies invasoras se están extendiendo en áreas en las que no son nativas). No obstante, hay un considerable solapamiento entre estas tres categorías, y un gran número de estas especies pueden ser clasificadas dentro de los tres grupos. Es este solapamiento el que garantiza que generalizaciones realizadas sobre una categoría puedan ser útiles para comprender el comportamiento de muchas (aunque no todas) especies pertenecientes a las otras dos. Hay que elaborar teorías que nos ayuden a establecer prioridades para el control de malas hierbas invasoras introducidas y nos permitan predecir el riesgo de futuras invasiones. Los análisis de las relaciones estadísticas entre los rangos de distribución nativos y no nativos de especies introducidas desde Eurasia a América y viceversa pueden proporcionar cierto entendimiento y generar interesantes hipótesis con respecto a la naturaleza de las especies invasoras. Por el momento, sólo existen generalizaciones muy limitadas, basadas en fisiología vegetal, genética, o demografía. Sin embargo, las invasiones de pinos (género Pinus) y, muy probablemente, otras especies leñosas de plantas con semillas son predecibles sobre la base de un pequeño número de caracteres biológicos simples. Estos resultados son prometedores y deberían estimularnos a continuar con esta línea de investigación.
PALABRAS CLAVE: Malas hierbas, invasoras, especies introducidas.

SUMMARY: Weeds, invaders, and colonizers are three closely related but not identical concepts reflecting three different viewpoints: anthropocentric (weeds interfere with management goals of people), ecological (colonizers appear early in successional series), and biogeographical (invaders are spreading into areas where they are not native). Nevertheless, there is a considerable overlap between these three categories, and a large number of obnoxious species can be cross-classified as belonging to all three. It is this overlap which guarantees that generalizations made about one category can be helpful in understanding the performance of many (but not all) species belonging to the other two. We need predictive theories which can help us set priorities for the control of introduced invasive weeds and allow us to predict the risk of future invasions. Analyses of statistical relationships between native and adventive distribution ranges of species introduced from Eurasia to Americas and vice versa can provide some understanding and generate interesting hypotheses concerning the nature of successful invaders. At present, only very limited generalizations are available, based on plant physiology, genetics, or demography. However, invasiveness of pines (genus *Pinus*) and, very likely, other woody species of seed plants is predictable on the basis of a small number of simple biological characters. These results are promising and should encourage us to continue with this line of research.
KEY WORDS: Weeds, invaders, introduced species.

INTRODUCTION

Weeds, invaders, and colonizers are three closely related but not identical concepts.

Although their definition and relationship are often only vaguely describes (BAKER & STEBBINS, 1965; DI CASTRI, 1990), they reflect three different viewpoints: anthropocentric (weeds interfere with management goals of people),

ecological (colonizers appear early in successional series), and biogeographical (invaders are spreading into areas where they are not native).

Some plant species are weeds because they are poisonous but they cannot be classified as colonizers or invaders (*Datisca glomerata*, *Aconitum* spp.). Some historically very important agronomic weeds are poor colonizers, so are now endangered species in some European countries (e.g., *Agrostema gitago*; SE-VENSSON & WIGREN, 1986). Colonizers are, in general, successful invaders, but only in disturbed environments (BAZZAS, 1986, RE-JMÁNEK 1989). Many invaders certainly become very serious weeds but some can hardly be classified as weeds in the usual sense (*Lygodium japonicum* in floodplain forests of Louisiana). However, all invaders in protected areas are usually classified as weeds (sometimes "ecological" or "environmental weeds") because in national parks and similar areas non-native species often interfere with the major management goal, i.e., protection of native biota.

Obviously, there is a considerable overlap between these three categories, and a large number of obnoxious species can be cross-classified as belonging to all three (Fig. 1). It is this overlap which guarantees that generalizations made about one category can be helpful in understanding the performance of many (but not all) species belonging to the other two. All invasive species I will mention in this paper are weeds in one sense or another and most of them are colonizers as well.

Historically, there was little concern about negative effects of exotic species introductions. Recently, however, "biological pollution" has become nearly as alarming as has chemical pollution in many areas of the earth. The negative effects of exotic mammals were recognized rather early (e.g., rodents, ungulates, and predators on oceanic islands). Also, a lot of attention has been paid to exotic agronomic and range weeds, especially in North America, since the beginning of this century (PARISH, 1920). However, it has been realized only recently that
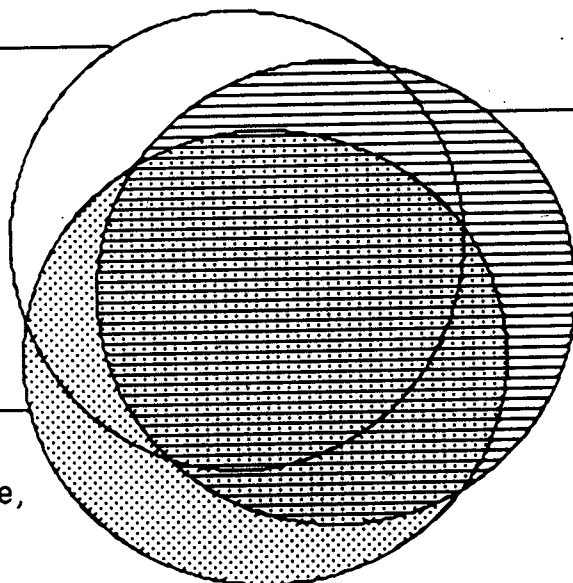

FIGURA 1: Weeds, Colonizers, and invaders are overlapping but not identical concepts reflecting three different view-points.

plant invaders may have far reaching ecosystem-level effects. *Ammophila arenaria* (European beach grass) was introduced for stabilization of coastal dunes in California and Oregon and is changing drastically the geomorphology of the dunes, creating an environment hostile for several native rare species. *Tamarix* species have drawn down the water table in many riparian and wetland sites in the US Southwest. In many parts of the world, the introduction of productive, fuel-producing but fire-tolerant grasses (e.g., *Andropogon virginicus, Schizachyrium condensatum*) has led to an increase in the frequency of fires and the elimination of fire-sensitive natives.

Exotic pines (*Pinus radiata, P. patula, P. halepensis*, etc.) are changing species-rich native shrubby vegetation (fynbos) to homogeneous, species-depauperated forests in southern Africa.

We need predictive theories which can help us set priorities for the control of introduced invasive weeds and allow us to predict the risk of future invasions. Unfortunately, pressing questions like "what attributes make some species more invasive?" or "what makes some ecosystems more invasible than others?" do not have satisfactory answers (BAKER & STEBBINS, 1965; KORNBERG & WILLIAMSON, 1987; DRAKE & al., 1989; GROVES & DI CASTRI, 1991; BARRETT, 1992; PERRINS & al., 1992). Useful generalizations are hard to develop because most of the data come from contingent qualitative observations. Moreover, data on failed invasion attempts are usually not available. Not surprisingly, the lack of progress in this area has fostered pessimism regarding the prospect of predicting which organisms are likely to become successful invaders (CRAWLEY, 1987; ROY, 1990).

In this paper will first show that analyses of statistical relationships between primary (native) and secondary (adventive) distribution ranges of species introduced from Eurasia to North America can provide some understanding and

generate interesting hypotheses concerning the nature of successful invaders. Then I will report that invasiveness of pines (genus *Pinus*) and, very likely, other woody species of seed plants is predictable on the basis of a small number of simple biological characters.

ANALYSES OF GEOGRAPHIC RANGES

Initially, comparison of native and adventive distributions of plants seems to be a simple matter. However, quantification and rigorous analyses of geographic ranges are beset by many problems (GASTON, 1991; RICKLEFS & LATHAM, 1992). Moreover, until publication of the 2nd edition of Hultén's Atlas (HULTÉN & FRIES, 1986), there had not been any satisfactory attempt to present native and adventive distributions in a consistent way for a large number of species. Only this publication allows us to analyze primary and secondary distributional patterns of many originally European species growing north of the tropic of Cancer.

I chose two of the largest families of angiosperms —Gramineae and Compositae— using primary distributions in Eurasia and northern Africa as they were published in the Atlas. Then I checked longitudinal limits of secondary distributions in North America using about 20 recently published local floras, making corrections for about 40% of the species. Unfortunately, I had to exclude some species (e.g., Digitaria sanguinalis) because of uncertain southern limits either in Eurasia or in North America. Finally, for all remaining species I made comparisons of their primary longitudinal ranges in Eurasia with secondary ones in eastern and western North America.

First, means of primary (native) latitudinal ranges of species naturalized in North America are significantly larger (about 100) than those of

species which have never been reported as naturalized in North America (Table 1). Remarkably, the two families provided almost identical results. Second, all regressions of secondary latitudinal ranges (in eastern and western North America) on primary latitudinal ranges (in Eurasia and northern Africa) are positive and highly significant (Figs. 2 & 3).

There is, however, a large amount of variance in the secondary latitudinal ranges which is not explained by the primary latitudinal ranges (R2 varies between 0.21 and 0.47). Diversity of life forms certainly contributes to the unexplained variance. Slopes of regression lines are greater for annuals and biennials than for perennials but not significantly. Residence time (time since the introduction) and number of introductions could confound latitudinal agreement for some species.

Some inherent biological differences can play a role as well. Compare *Poa bulbosa, Alopecurus pratensis, Corynephorus canescens,* and *Molinia caerulea* whose secondary latitudinal ranges are below ±50 intervals along regression lines with *Poa compressa, Lolium multiflorum, Agrosteis tenuis,* and *Festuca arundinacea* with secondary latitudinal ranges above ±50 intervals along regression lines for both eastern and western North America. Also, compare, *Filago arvensis, Eupatorium canabinum, Lactuca muralis* and *Tusilago farfara* below with *Crepis tectorum, Hypochoeris radicata, Sonchus arvensis,* and *Hieracium au-*

rantiacum above ±50 intervals. From this analysis it follows that severall potentially serious invaders still have a limited distribution in North America (*Apera spica-venti, Bromus arvensis, Calamagrostis epigeios, Carduus crispus, Tusilago farfara*).

There are two explanations why there should be a positive correlation between primary and secondary geographic ranges. FORCELLA & WOOD (1984) and FORCELLA & al. (1986) concluded that the positive relation between area of native distribution and invading capacity arose from the fact that the propagules of widespread species have a higher probability of transport to other countries or continents. On the other hand, NOBLE (1989) and ROY & al. (1991) inclined to the opinion that, with the considerable increase in intercontinental exchange since the beginning of this century, invasion by a species depends more on the interaction between its biological properties and those of the recipient region than on the probability of reaching that region. ROY & al. (1991) suggested that the same biological traits that enable some species to spread across their native continents (and across different climatic zones) also make them able to invade new continents. Only rigorous introduction experiments and/or analyses of well documented invasions over long periods of time (decades) can help to decide which of these two explanations is more likely correct.
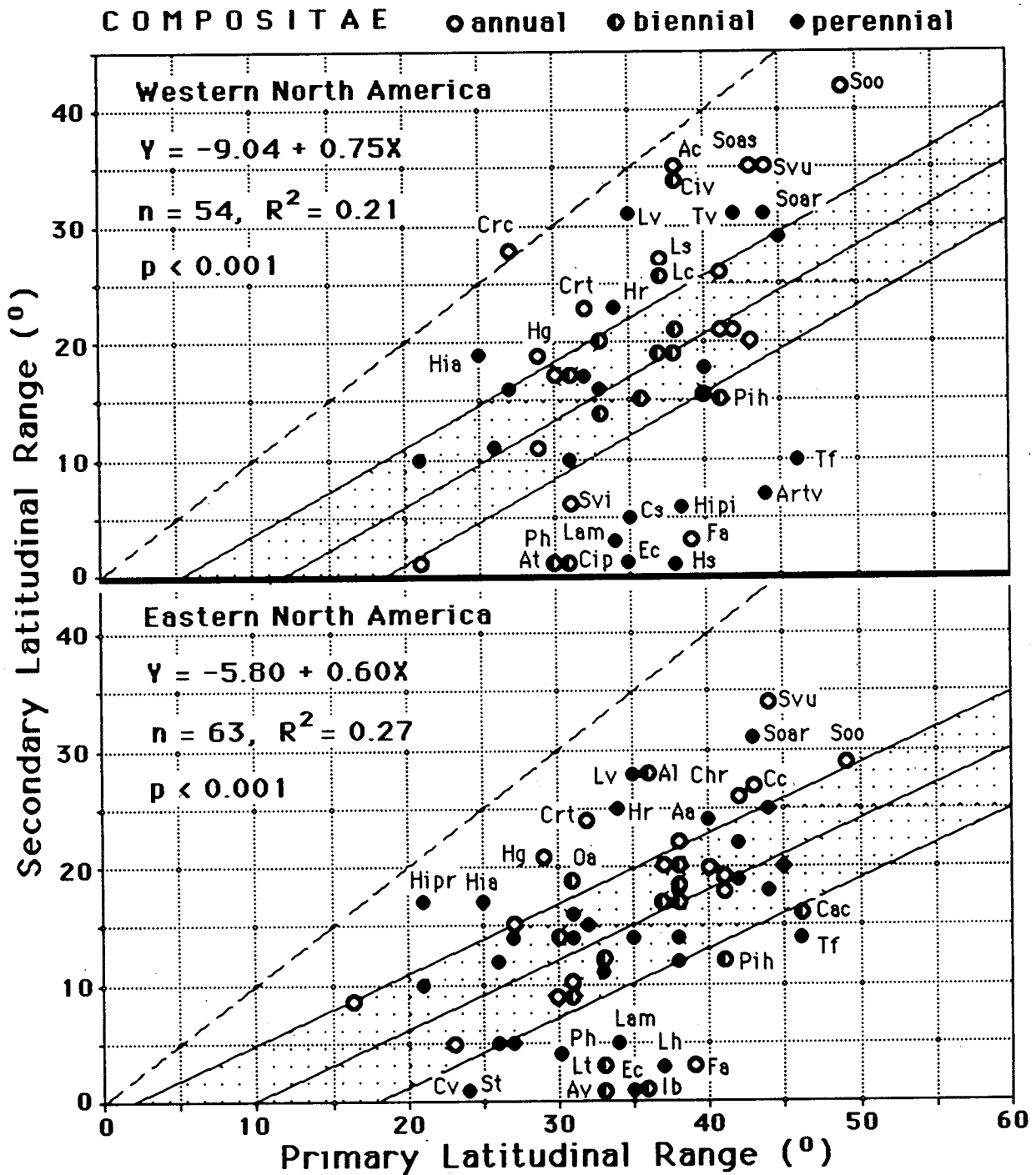
Secondary latitudinal ranges of species introduced in North America are in general about

	Mean primary latitudinal range	
	Species naturalized in North America	Species not naturalized in North America
Gramineae	36.7 (SD = 7.3, n = 61)	25.6 (SD = 8.0, n = 42)
Compositae	34.6 (SD = 7.2, n = 64)	25.3 (SD = 10.4, n = 63)

TABLE 1: Mean primary latitudinal ranges (°) of Gramineae and Compositae species in Eurasia and northern África calculated separately for species which are and are not naturalized in North America. Means in rows are significantly different (two tailed t-test, p < 0.001).
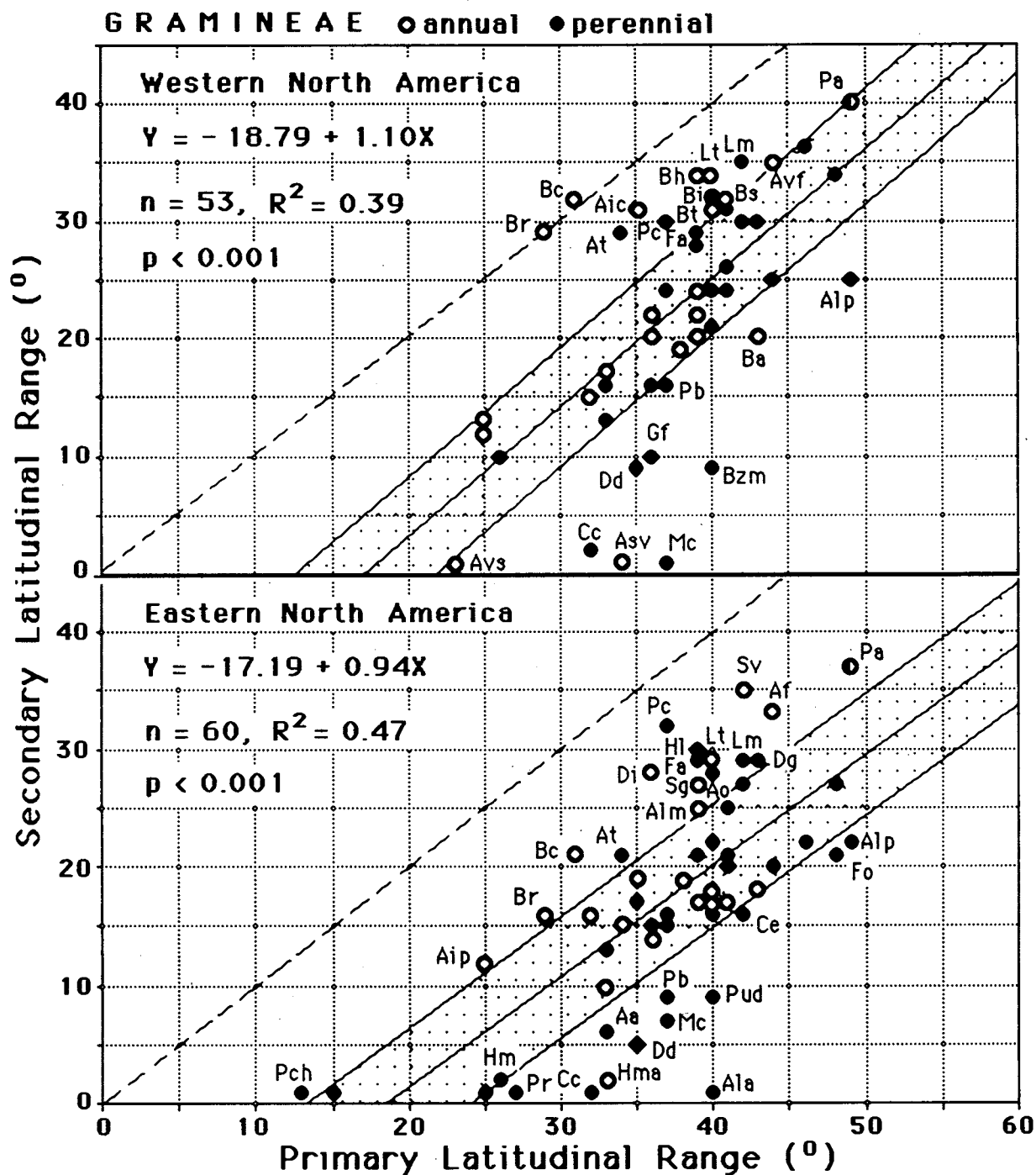
FIGURA 2: Relationship between primary (Eurasia/Africa) and secondary (eastern and western North America) latitudinal ranges of grasses introduced to North America. Dashed lines represent identical latitudinal ranges in compared regions. Species above ±5° intervals along regression lines: Aic = *Aira caryophyllea*, Aip= *A. praecox*, Alm = *Alopecurus myosuroides*, Ao = *Anthoxanthum odoratum*, At = *Agrostis tenuis*, Avf = *Avena fatua*, Bc = *Bromus commutatus*, Bh = *B. hordeaceus (B. mollis)*, Bi = *B. inermis*, Br = *B. ramosus*, Bs = *B. secalinus*, Bt = *B. tectorum*, Dg = *Dactylis glomerata*, Di = *Digitaria ischaemum*, Fa = *Festuca arundinacea*, Hi = *Hoicus lanatus*, Lm = *Lolium multiflorum*, Lt = *L. temulentum*, Pa = *Poa annua*, Pc = *P. compressa*, Pch = *P. chaixii*, Sg = *Setaria glauca*, Sv = *S. viridis*. Species below ±5° intervals along regression lines- Aa = *Ammophila arenaria*, Ala = *Alopecurus arundinaceus*, Alp = *A. pratensis*, Asv = *Apera spica-venti*, Avs = *Avena strigosa*, Ba = *Bromus arvensis*, Bzm = *Briza media*, Cc = *Corynephorus canescens*, Ce = *Calamagrostis epigeios*, Dd = *Danthonia decumbens*, Fo = *Festuca ovina*, Gf = *Glyceria fluitans*, Hm = *Holcus mollis*, Hma = *Hordeum marinum*, Mc = *Molinia caerulea*, Pb = *Poa bulbosa*, Pr = *P. remota*, Pud = *Puccinellia distans*.

COMPOSITAE ○ annual ◑ biennial ● perennial

Western North America

$Y = -9.04 + 0.75X$

$n = 54, \quad R^2 = 0.21$

$p < 0.001$

Eastern North America

$Y = -5.80 + 0.60X$

$n = 63, \quad R^2 = 0.27$

$p < 0.001$

Secondary Latitudinal Range (°)

Primary Latitudinal Range (°)

FIGURA 3: Relationship between primary (Eurasia/Africa) and secondary (eastern and western North America) latitudinal ranges of Compositae species introduced to North America. Dashed lines represent identical latitudinal ranges in compared regions. Species above ±5° intervals along regression lines: Aa = *Artemisia absinthium*, Ac = *Anthemis cotola*, Al = *Arctium lappa*, Cc = *Centaurea cyanus*, Chr = *Chamomilla recutita*, Civ *Cirsium vulgare*, Crc = *Crepis capillaris*, Crt = *C. tectorum*, Hg = *Hypochoeris glabra*, Hr = *H. radicata*, Hia = *Hieracium aurantiacum*, Hipr = *H. pratense*, Lc = *Lapsana communis*, Ls = *Lactuca serriola*, Lv = *Leucanthemum vulgare*, Oa = *Onopordon acanthium*, Soas = *Sonchus asper*, Soar = *S. arvensis*, Soo = *S. oleraceus*, Svu = *Senecio vulgaris*, Tv = *Tanacetum vulgare*. Species below ±5° intervals along regression lines: Artv = *Artemisia vulgaris* ssp. *vulgaris*, At = *Arctium tomentosum*, Av = *A. vulgare*, Cac = *Carduus crispus*, Cip = *Cirsium palustre*, Cs = *Centaurea scabiosa*, Cv = *Carlina vulgaris*, Ec = *Eupatorium canabinum*, Fa = *Filago arvensis*, Hipi = *Hieracium pilosella*, Hs = *H.* group *Silvaciformia*, Ib = *Inula britanica*, Lam = *Lactuca muralis*, Lh = *Leontodon hispidus*, Lt = *L. taraxacoides*, Plh = *Picris hieracioides*, Ph = *Petasites hybridus*, Svi = *Senecio viscosus*, St = *Serratula tinctoria*, Tf = *Tusilago farfara*.

20° narrower than their native ranges in Eurasia and northern Africa. The major resistance against expansion of exotic plant species in North America seem to be of an abiotic nature: low temperatures in the north and drought in the southwest (Fig. 4). Biotic resistance (competition) which could be potentially most important in the southeast is obviously suppressed by large-scale human disturbance.

For 20 plant species introduced from North America to Eurasia I did not find any significant relationship between their primary and secondary latitudinal ranges (R2 < 0.01). Perhaps introductions in this direction are more recent and
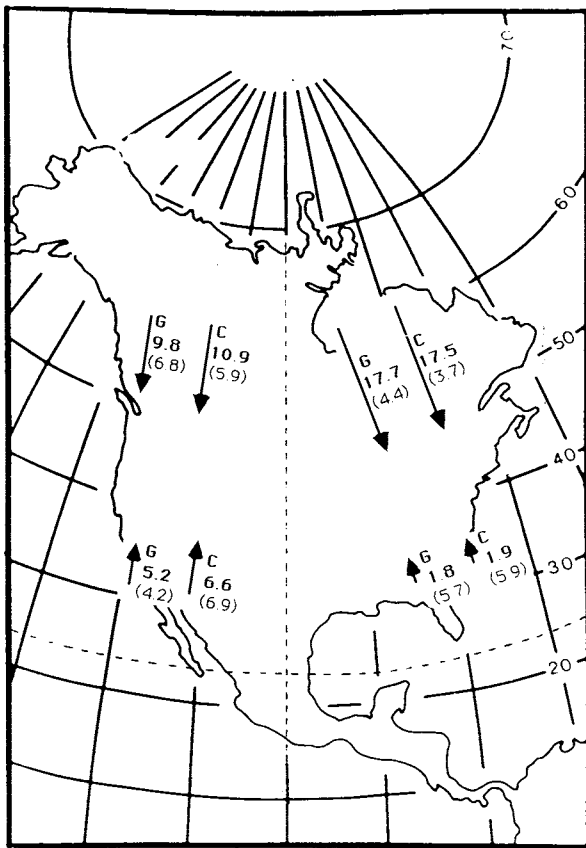
FIGURA 4: Resistances of the North American continent to European plant invasions quantified as mean differences (expressed as arrows) between latitudinal limits of Gramineae (G) and Compositae (C) species in Eurasia and in eastern and western North America. Bold numbers represent mean differences in degrees, numbers in parentheses are standard deviations. Note that minimum SDs are associated with maximum resistance in the northeast.

adventive geographic ranges are still not stabilized. Also, data on more species introduced from North America to Eurasia are needed to make more reliable conclusions. Unfortunately, precise southern limits of native distributions of many species introduced from North America are not known.

Analyses of primary and secondary geographic ranges can generate stimulating hypotheses, but these should be used with caution for identifying potential invaders. *Pinus radiata* and *P. muricata* are among the most invasive weeds of the Southern Hemisphere; their native geographic ranges, however, are very narrow (CRITCHFIELD & LITTLE, 1966). In general, it is true that invasive pine species (see below) have greater mean longitudinal range (1 6.30, SD = 9.6, n = 1 2) than non-invasive pine species (1 0.40, SD = 5.2, n = 12). However, the difference is not significant (p > 0.05). Something more essential must be responsible for striking differences between invasive and non-invasive pine species.

INVASIVE PINES HAVE PREDICTABLE CHARACTERS

Characters responsible for remarkable differences in invasiveness of some pine species were analyzed by REJMÁNEK & RICHARDSON (1992).

There are several reasons why the genus *Pinus* represents a unique opportunity for this type of study. Pines form a clearly defend genus in the Northern Hemisphere with at least 90 species. Pines are economically important, or at least promising, and many species have been introduced to almost all countries with climates reasonably similar to areas of their native distribution. Life history characters of many species have been studied in detail. Reliable records about individual introductions in terms of

failures, survival, growth, regeneration, and spread are extensive. There are species of pines with clearly weedy behavior in many countries (especially in the Southern Hemisphere) and species frequently planted but never reported as spreading. Finally, pine reproduction biology is relatively simple, and underlying trends which can be masked by intricacies of pollination and seed dispersal in angiosperms can be more easily determined.

Our analyses of characters responsible for species invasiveness were based on data available for 24 well known and frequently cultivated pine species (Table 2). We classified 12 of them as invasive *a priori* (reported as spontaneously spreading on at least two continents) and 12 as non-invasive (planted on at least three conti-

nents but never reported as spreading). Ten life-history characters were included in the analysis initially- mean height, maximum height, minimum juvenile period, mean longevity, mean seed mass, seed-wing loading index, average percentage of germination, mean interval between large seed crops, degree of serotiny, and fire tolerance index.

A simple discriminant analysis was performed using these characters as predictors of membership in the two groups. Only three characters contributed significantly to the discriminant function and consistently maximized the difference between the two groups: (mean seed mass), (minimum juvenile period), and mean interval between large seed crops (Table 2). The stability of the classification was further

| | Sub genus *Pinus* | | | Sub genus *Strobus* | | |
	Species	Z score		Species	Z score
Invasive species					
Lodgepole	*contorta*	9.85			
Monterey	*radiata*	7.79			
Aleppo	*halapensis*	7.50			
Mexican weeping	*patula*	6.86			
Jack	*banksiana*	6.82			
Maritime	*pinaster*	6.73			
Bishop	*muricata*	6.57			
Scotch	*sylvestris*	5.44			
Slash	*elliotii*	3.44			
Austrian	*nigra*	1.28	Eastern	*strobus*	1.11
Non-invasive species					
Pitch	*rigida*	-0.43			
Caribbean	*caribea*	-1.33			
Red	*resinosa*	-1.64			
Coulter	*coulteri*	-4.06	Limber	*flexilis*	-1.68
Torrey	*torreyana*	-5.65	Pinyon	*edulis*	-6.87
Longleaf	*palustris*	-5.99	Sugar	*lambertina*	-9.21
Digger	*sabiniana*	-6.96	Swiss stone	*cembre*	-9.81
			Mexican pinyon	*cembroides*	-10.13

TABLE 2: Discriminant nalysis of invasiveness in frequently cultivated species of'soft' (subgenus *Strobus*) pines, Based in empirical evidence, 12 species were *a priori* classified as invasive and 12 as non-invasive. A function (Z) discriminating most successfuly between these two groups combines mean seed mass in mg (M), mean interval between large seed crops in yr (C), and minimum juvenile period in yr (J): Z = 16.25 - 0.438 M - 2.089 J - 1.44C, F = 19.33, p < 0.001, relative contributions of M, J, and C are 43.3%, 28.4%, and 28.2%.

checked by 500 cross-validation runs where on-ly 6 species (50%) from each group were cho-sen randomly each time. Results indicate an unusual robustness of the classification (RE-JMÁNEK & RICHARDSON, 1992).

Two variables incorporated into the discri-minant function are rather straightforward: short juvenile period and short interval between large seed crops mean early and constant repro-duction. Small mean seed mass seems to be associated with several potentially important phenomena: larger number of seeds produced, better dispersal, high initial germinability, and shorter chilling period needed to overcome dor-mancy. The three selected variables point to an underlying r-K selection continuum (early-late successional roles) along which invasive-non-in-vasive pine species are situated.

Invasive species are clearly concentrated in the subgenus *Pinus* (*Diploxylon*) and non-inva-sive species in the subgenus *Strobus* (*Haplo-xylon*). Membership in a subgenus therefore can be used as a first indication of possible invasive-ness. The five most invasive pines, as they are known from literature and our own experience (*P. radiata, contorta, halepensis, patula, pinas-ter*), have the highest discriminant scores and in the course of all cross-validation runs were always correctly classified as invasive.

We next applied the discriminant function (Table 2) to 34 different and, in general, less of-ten cultivated species in the same genus. Poten-tially invasive species were again concentrated in subgenus *Pinus*. That at least some of the species with positive discriminant scores are po-tentially invasive is indicated by a number of pu-blished records of natural regeneration in countries of introduction. In fact, some of these species *(P. kesiya, thunbergiana, taeda)* could already be classified as invasive. Natural regene-ration and spread of two "non-invasive" species with large seeds *(P. koraiensis, pinea)* are faci-litated by their dispersal by native or introduced squirrels. Not surprisingly, the general trend re-vealed by the discriminant function can be

modified by species- and/or habitat-specific factors.

There are reasons to believe that the discri-minant function derived in this study may be applicable to other groups of woody seed plants. Among gymnosperms, all species in the frequently cultivated genus *Araucaria* are co-rrectly classified as non-invasive. On the other hand, *Picea sitchensis* (Sitka spruce) and *Larix decidua* (European larch) are correctly predic-ted to be invasive. An application of the discri-minant function to 40 of the most invasive woody angiosperm species from 40 different genera resulted in correct classification of 39 species. Only *Melia azedarach* was incorrectly classified as non-invasive. Efficient bird disper-sal seems to be responsible for this discrepancy. Using the "pine discriminant function", many frequently cultivated but non-invasive angios-perm species *(Acer saccharum, Quercus* spp., *Fagus* spp., *Magnolia* spp., *Carya* spp., *Aescu-lus* spp., *Juglans* spp., *Corylus* spp.) are correc-tly classified as non-invasive. However, some non-invasive species of *Populus* (*P. tremula, tremuloides*) are classified as invasive. The short seed viability and high seedling mortality brought about by the slow growth of seedling primary roots in these species prevent them from becoming invasive. In general, it appears that invasiveness of woody species with dry fruits and mean seed mass <2.0 mg -*Populus* spp., *Salix* spp., *Betula* spp., *Alnus* spp., *Mela-leuca quinquenervia*- is very often limited to wet habitats. Vertebrate dispersal is responsible for success of many woody invaders (HA-YASHIDA, 1989; RICHARDSON, & al. 1990; BASS, 1990; GADE, 1976; TIMMIS & WI-LLIAMS, 1987; VITOUSEK & WALKER, 1989). This fact is taken into account in Table 3.

Self-pollination or pollination niche separa-tion can be important in initial stages of some invasions (BAKER, 1967; PARRISH & BAZZAZ, 1978). Several structural and physio-logical characters like bark thickness (RI-CHARDSON & al., 1990), symbiotic nitrogen

fixation (VITOUSEK & WALKER, 1989), shade tolerance (JONES & MCLEOD, 1989), or stem photosynthesis (BOSSARD & REJMÁNEK, 1992) may contribute to the success of some invaders in extreme environments. Nevertheless, keeping possible exceptions in mind, the discriminant function derived from simple demographic parameters of invasive and non-invasive pines, together with tentative general rules summarized in Table 3, seem to be the first really general screening tool for detection of invasive woody seed plants. These results are promising and should encourage us to continue with this line of research.

ACKNOWLEDGMENTS

REFERENCES

BAKER, H.G. (1967). The evolution of weedy taxa in the *Eupatorium* microstemon species aggregate. **Taxon** 16:293-300.

BAKER, H.G. & STEBBINS, G.L. (1965). **The Genetics of Colonizing Species.** Academic Press, New York.

BARRETT, S.C.H. (1992). Genetics of weed invasions. in: S.K. Jain & L.W. Botsford, (eds). **Applied Population Biology.** pp. 91-119. Kluwer Academic Publishers, Dordrecht.

BASS, D.A. (1990). Dispersal of an introduced shrub (*Crataegus monogyna*) by the Brush-tailed Possum (*Trichosurus vulpecula*). **Austral. J. Ecol.** 15:227-229.

BAZZAZ, F.A. (1986). Life history of colonizing plants: some demographic, genetic, and physiological features. In: H.A. MOONEY & J.A. DRAKE, (eds). **Ecology of Biological Invasions of North America and Hawaii.** pp. 96-110. Springer-Verlag, New York.

BOSSARD, C. & REJMÁNEK, M. (1992). Why have green stems? **Funct. Ecol.** 6:197-205.

CRAWLEY, M.J. (1987). What makes a community invasible? In: A.J. GRAY, M.J. CRAWLEY & P.J. EDWARDS, (eds). **Colonization, Succession, and Stability.** pp. 429-453. Blackwell, Oxford.

		Opportunities for vertebrate dispersal	
		Absent	Present
Z > 0	Dry fruits and seed mass > 2 mg	Likely invasive	Very likely invasive
	Dry fruits and seed mass < 2 mg	Likely invasive in wet habitats	
	Fleshy fruits	Unlikely invasive	
Z < 0		Non-invasive	Possibly invasive

TABLE 3: Tentative general rules for detection of invasive woody seed plants based on values of the discriminant function Z, seed mass values, and presence or absence of opportunities for vertebrate dispersal. Z = 16.25 - 0.438 M - 2.089 J - 1.44C, M = mean seed mass in mg, J = minimum juvenile period in yr, C = mean interval between large seed crops in yr.

CRITCHFIELD W.B. & LITTLE, E.L. (966.) **Geographic distribution of the pines of the world.** US Department of Agriculture, Forest Service, Washington, D.C., Misc. Publ. 991.

DI CASTRI, A.J. (1990). On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: A.J. DI CASTRI; A.J. HANSEN & M. DEBUSHE, (eds). **Biological Invasions in Europe and the Mediterranean Basin.** Kluwer, Dordrecht.

DRAKE, J.A.; MOONEY, H.A.; DI CASTRI, F.; GROVES, R.H.; KRUGER, F.J.; REJMÁNEK, M. & WILLIAMSON, M. (1989). **Biological Invasions.** A Global Perspective. John Wiley, Chichester.

FORCELLA, F. & WOOD, J.T. (1984). Colonization potentials of alien weeds are related to their 'native' distributions: Implications for plant quarantine. **J. Austral. Inst. Agr. Sci.** 50:35-40.

FORCELLA, F.; WOOD, J.T. & DILION, S.P. (1984). Characteristics distinguishing invasive weeds within Echium (Bugloss). **Weed Res.** 26:351-364.

GADE, D.W. (1976). Naturalization of plant aliens: the volunteer orange in Paraguay. **J. Biogeogr.** 3:269-279.

GASTON, K.J. (1991). How large is a species' geographic range? **OIKOS** 61:434-438.

GROVES, R.H. & DI CASTRI, F. (1991). **Biogeography of Mediterranean Invasions.** Cambridge University Press, Cambridge.

HAYASHIDA, M. (1989). Seed dispersal by Red Squirreis and subsequent establishment of Korean Pine. **For. Ecol. Manage.** 28:115-129.

HUITÉN, E. & FRIES, M. (1986). **Atlas of North European Vascular Plants North of the Tropic of Cancer. Vols. 1, 2, 3.** Koeltz Scientific Books, Königstein.

JONES, R.H. & MCLEOD, K.W. (1990). Growth and photosynthetic responses to a range of light environments in Chinese Tallowtree and Carolina Ash Seedlings. **Forest Sci.** 36:851-862.

KORNBERG, F.R.S. & WILLIAMSON, M.H. (1987). **Quantitative Aspects of the Ecology of Biological Invasions.** The Royal Society, London.

NOBLE, I.R. (1989). Attributes of invaders and the invading process-terrestrial vascular plants. In: J.A. DRAKE & al. (eds). **Biological Invasions.** pp. 301-313. A Global Perspective. John Wiley, Chichester.

PARRISH, J.A.D. & BAZZAZ, F.A. (1978). Pollination niche separation in a winter annual community. **Oecol.** 35:133-140.

PARISH, S.B. (1920). The immigrant plants of southern California. **Bull. South. Calif. Acad. Sci.** 14:3-30.

PERRINS, J.; WILLIAMSON, M. & FITTER, A. (1992). A survey of differing views of weed classification: implications for regulation of introductions. **Biol. Conserv.** 59:47-56.

REJMÁNEK, M. (1989). Invasibility of plant communities. In: J.A. DRAKE & al. (eds). **Biological Invasions.** A Global Perspective. pp. 369-388. John Wiley, Chichester.

REJMÁNEK, M. & RICHARDSON, D.M. (1992). **Exotic pines reveal predictable characters of invasive species.** (Submitted).

RICHARDSON, D.M.; COWLING, R.M. & LE MAITRE, D.C. (1990). Assessing the risk of invasive success in Pinus and Banksia in South African mountain fynbos. **J. Veg. Sci.** 1:629-642.

RICKLEFS, R.E. & LATHAM, R.E. (1992). Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. **Amer. Nat.** 139:1305-1321.

ROY, J. (1990). In search of the characteristics of plant invaders. In: A.J. DI CASTRI; A.J. HANSEN & M. DEBUSH(eds). **Biological Invasions in Europe and the Mediterranean Basin.** pp. 335-352. Kluwer, Dordrecht.

ROY, J.; NAVAS, M.L. & SONIÉ, L. (1991). Invasion by annual brome grasses: a case study challenging the homoclime approach to invasions. In: GROVES, R.H. & F. DI CASTRI (eds). **Biogeography of Mediterranean Invasions.** pp. 207-224. Cambridge University Press, Cambridge.

SEVENSON, R. & WIGREN, M. (1986). A changing flora - a matter of human concern. Acat Univ. Ups., **Symb. Bot. Ups.** 27:241-251.

TIMMINS, S.M. & WILLIAMS, P.A. (1987). Characteristics of problem weeds in New Zealand's protected natural areas. In: D.A. SAUNDERS & al. (eds). **Nature Conservation: The Role of Remnants of Native Vegetation.** pp. 241-247. Surrey Beatty & Sons in association with CSIRO and CALM.

VITOUSEK, P.M. & WALKER, L.R. (1989). Biological invasion by Myrica faya in Hawaii- plant demography, nitrogen fixation, ecosystem effects. **Ecol. Monogr.** 59:247-265.