# THE ECOLOGICAL CHARACTERISTICS OF ALIENS IN NATURAL AND SEMI-NATURAL STANDS*

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## General Remarks

Alien means foreigner, immigrant or stranger. However, alien plants do not of course have nationalities or borders, as do countries. In the case of Japan, all plants and animals that immigrated from outside are foreign or exotic because Japan is a chain of islands surrounded by the sea. However, in the case of a continent of many countries, plants and animals move freely regardless of the boundaries of countries. GATES (1940) verified the movement of plants with a direction by the inventory of plants with an interval of 50 years.

There are archeotypes or prehistoric naturalized plants (Maekawa 1943), such as *Lycoris radiata* and other weeds that accompanied the introduction of crops (rice in the Yayoi Period, starting in the 2nd century AD and lasting for several centuries, and later, wheat, barley, rape and others. In the Edo Era(1603−1867), Japan was politically closed, and even plants could not immigrate from outside. Against such a historical background, the record of plant invasion into Japan is relatively clear. At the beginning of the Meiji Era(1868−1912), there were about 20 new aliens excluding the prehistorical ones, and after that 132 species in 1936, 236 in 1951, and 800 in 1970 have been identified (KASAHARA 1975). On the Island of Oahu, Hawaii, more than two thousand cultivated and naturalized plants have been added to an original flora of scarcely one thousand species (EGLER 1942). At any rate, the addition or dispossission of aliens to or from indigeneous flora is a

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characteristic result of human impact.

## Weeds, Aliens and Pioneers

As stated earlier (NUMATA 1976a), weeds, aliens and pioneers have common ecological characteristics. "Weeds and Aliens" by SALISBURY (1961) shows this. Agricultural weeds are essentially migratory cosmopolitan. In their original homes they are mild under predators and pests, but the overrun competiotors freely without the limitations of predators and pests in their new habitat. Aliens were divided into aliens in natural habitats (neophyte—this is sometimes understood as aliens in general, PIJL 1969), aliens in man-made habitats (apophyte or epoekoptyte—this is sometimes ruderal plants gregariously growing in man-made habitats, PIJL 1969) and temporary aliens (ephemerophyte)(THELLUNG 1915).

It may be difficult for aliens to invade a natural stand such as *Leucaena leucocephala*. However, African snails have infested disturbed sites in the Bonin Islands (NUMATA and OHSAWA 1970). However, *Spartina townsendii* (natural hybrid of *S. maritima* indigeneous in the salt marsh of U.K. with *S. alterniflora* naturalized from North America) grows lustily changing a part of the British landscape. This hybrid was re-naturalized in North America and said to have exterminate the original species of *S. maritima* (ELTON 1958).

SUKOPP (1960) divided aliens into two groups. 1) naturalization becoming a constituent of indigeneous plant communities (Einpassung), and 2) displacing indigeneous spesies and taking leadership in a new plant community (Verdrägung). The former is a membership naturalization, and the latter is a displacement naturalization. Most naturalization in Japan is membership naturalization. such as *Veronica arvensis*, *Euphorbia maculata*, *Trifolium repens*, *Bromus catharticus* in semi-natural communities of weeds, but there are a few cases of displacement naturalization by an overwhelming dominant, such as *Ambrosia artemisiifolia*, *Erigeron annuus*, *E. canadensis*, and *Solidago altissima*. On the other hand, there are problems of ecesis risistance and ecological homeostasis seen from the viewpoint of the accepting communtities (NAGI 1964).

The relationship of the indigeneous versus the aliens is as above. However, there is another case of the establishment of new communities in vacant niches (EGLER 1942)."In the original flora of the Hawaiian islands, there were apparently no plants to occupy shallow ocean shores, which occur around the mouths of rivers and behind bay bars.

Plants such as *Sesuvium portulacastrum*, though locally common on low-lying sands, has not been observed to thrive on continuously submerged sites. Consequently, *Batis maritima* introduced previous to 1895, found an ecological niche apparently unoccupied. It became "aggressive", forming pure communities in shallow water, and probably displacing no seed plant, alien or native. More recently, several species of mangrove have been introduced (including *Brugiera sexangula*, *B. parviflora* and *Rhizophora mucronata*.) These plants are adapted not only for the *Batis* sites, but aslo for areas of deeper water. The pioneer-like characteristics of aliens and weeds have originated from the easiness of their invasion in early stages of secondary succession. In the seed bank dynamics in the soil corresponding to progressive succession, seeds of pioneer plants decrease (OOSTING and HUMPHREYS 1940, NUMATA et al. 1964) as well as do weeds (WARINGTON 1958).The ecological characteristics of aliens (NUMATA 1976) are 1) the production of many small, light seeds (*Erigeron* spp.), 2) not small seeds but wide dispersal by birds (*Ambrosia* spp.), 3) strong competibility based on rapid early growth after germination (annuals, winter annuls), 4) the long life-span of seeds of some species (*Oenothera* spp.) in the soil, 5) the wide range of seed germination, such as facultative light germination by *Ambrosia* spp., 6) mostly sun plants, 7) having rather large plasticity and resistance to environmental conditions, such as temperature, day length, soil condition, etc., 8) high density regulation ability—intraspecific and interspecific, such as self-thinning at high density or supplementary germination of new individuals at a low density, 9) occassional vegetative propagation by rhizomes (*Solidago* spp.), 10) the excretion of allelopathic substances to a preceding dominant (*Ambrosia* vs. *Erigeron*, etc.) and 11) the polymorphy or heteromorphy of seeds in Compositeae, Chenopodiaceae, Leguminoseae, Brassicaceae and Gramineae also seen in weediness (HARPER 1965). Polymorphic or heteromorphic seeds have different ecological characteristics, and have a wide range of growth in their habitats and in their germination periods.

Many naturalized annuals are weeds in farmlands and prehistorically naturalized plants. Some of them are not agricultural weeds in mountain pastures, such as *Erigeron annuus* and *Rumex obtusifolius*. *Erigeron annuus*, *E. canadensis*, *E. philadelphicus*, *E. strigosus* etc. are naturalized plants as a dominant of ruderal vegetation or component of mountain grasslands. These are not agricultural weeds in farmlands, but are weedy species in man-made and semi-natural pastures and meadows in Japan (SAKAI et al. 1975).

I studied coastal vegetation on a sand bar stretching westward in Tokyo Bay (NUMATA 1949) on which *Zoysia macrostachya* community was distributed in the southern coast. In the zone next to the frontal *Zoysia* zone, an alien zone with *Erigeron canadensis* and *Oenothera erythrosepala* invaded. Howerer, after a typhoon, they collapsed, but then renewed their invasion. Repeating this phenomenon, they could establish an alien zone on the back of the frontal *Zoysia* zone. Another interesting fact is that *Oenothera laciniata* displaced *P. erythrosepala* and has become a dominant there.

In Hokkaido, except for the southern Oshima Peninsula, *Poa pratensis* is a widely distributed dominant in pastures. This is a non-indigeneous species, however it makes up a typical vegetation type of grassland in Hokkaido. Under light grazing, a dwarf bamboo pasture is established with *Sasa veitchii* and *Sasa nipponica*, however under moderate and heavy grazing, *Poa pratensis* pastures are established as a semi-natural pasture as well as a man-made pasture. This is a very rare case in Japan.

As a similar case, some of bamboo forests in Japan seem to have been introduced from China. *Phyllostachys bambusoides* and *P. nigra* var. *henonis* seem to be indigeneous, however *P. pubescens* was definitely introduced from China through the Ryukyu Islands. There are many cultivated stands but there are also newly propagated semi-natural stands that have not been cultivated. In this case, bamboo stands which dominant is an alien naturally cover a wide area.

## Bamboos

In Japan, bamboos have been cultivated widely from early times. Fossils of *Phyllostachys bambusoides* and *P. nigra* var. *henonis* were said to have been found in Japan in the Miocene and Diluvial epochs (KOIZUMI 1942). However, there is another opinion that the native home of *P. bambusoides* is China (MCCLURE 1948).

It is not clearly known whether or not bamboo cultivation was as prosperous as it is today, however bamboo cultivation for the protection of river banks was recommended in the 16th century (UEDA 1955). Man-made bamboo forests were fertilized in the 17th century, after which bamboo attained its character as s cultivated plants. Among them, *P. pubescens* was as stated above introduced between 1832 and 1836 to Kagoshima, southern Kyushu from China through the Ryukyu Islands.

However, at the present time, there are some natural bamboo forests on mountain-

sides. A bamboo stand we studied in Kyoto (UEDA and NUMATA 1961) was a good example of such a natural one. A bamboo stand on steep slopes of 45 degrees facing southeast 500 m in alt. was actually a natural forest composed of *Phyllostachys nigra* var. *henonis* and *P. bambusoides*, the distributional pattern of which was quite random. Such random distribution is maintained through gains and losses every year as density regulation. In this sense, natural bamboo stands on steep slopes are in dynamic equilibrium and so are considered to be a topographical climax.

However, bamboos are almost all under cultivation in Japan, and some of them are in a semi-natural state of secondary successin on wastelands (KURAUCHI 1952). Even in a plantation, we could see a semi-natural community in the control plot without management in a field experiment (NUMATA and OGAWA 1959). During the experiment, the biomass of bamboos and the crown density gradually decreased, and the relative light intensity under the canopy increased. Then, the dominance of species competitive with bamboo, such as dwarf bamboo (*Pleioblastus chino*), *Miscanthus sinensis*, etc. increased, and secondary succession proceeded to the *Pinus densiflora* stage.

*Phyllostachys pubescens*, as a true alien, is usually cultivated, but in some cases as in the topographical climax or semi-natural stands, it shows an ecological situation to other species of *Phyllostachys*. When a *P. pubescens* stand grows with its neighbour *Cryptomeria japonica* stand, a mixed conifer-bamboo stand is easily formed, because the habitat conditions of soil, water and light are similar.

## Trachycarpus

Two species of *Trachycaropus*, *T. excelsa* (windmill palm) and *T. fortunei* (fortune palm) are widely cultivated in gardens, particularly in the southern half of Japan. Since 1950, we have studied preserved natural forests in the Nature Study Park in the center of Tokyo, a typical urban forest. There were *Castanopsis cuspidata* var. *sieboldii* forest, *Quercus serrata* forest, *Pinus thunbergii* forest, *Cornus controversa* forest and others (NUMATA and TEZUKA 1966). After the war, the above two species of *Trachycarpus* introduced from the home gardens around the Nature Study Park by birds. *T. excelsa* are said to have originated in Southern Kyushu, however we cannot find its indigeneous growing place, and *T. fortunei* originated in South China. Both species have been introduced from neighboring residential areas into the natural forests of *Castanopsis*

*cuspidata* var. *sieboldii*, *Pinus thunbergii*, etc. where they showed patchy distribution with few lobed growth forms compared with the normal growth form (ODAKI and IWASE 1966).

*Trachycarpus* spp. were originally not included in the undergrowth of natural forests in the vicinity of Tokyo. They were introduced from outside by birds, such as *Hypsipetes amaurotis* (the brown-eared bulbal). The bird was observed to swallow more than 100 seeds per day. Those seeds are released from the bird's body as excrement 1−2 hours after swallowing them. The germination of seeds is as high as 83% (HAGIWARA 1977). The bird avoids *Pinus densiflora*, *P. thunbergii*, *Cryptomeria japonica*, *Castanopsis cuspidata* var. *sieboldii*, etc. and approaches to *Aphananthe aspera*, *Cornus controversa*, *Celtis sinensis* var. *japonica*, etc. Therefore, the saplings and seedlings are contagiously distributed according to the distribution of tree species (HAGIWARA 1979). The growth from is impoverished under a closed canopy as mentioned above, however the tolerance of seedlings is as high as 0.1−0.3% under relative light intensity for the compensation point (HAGIWARA 1980).

## Pinus lutchuensis

In the Bonin Islands, there is only one native conifer, *Juniperus taxifolia*. *Pinus lutchuensis* was introduced in 1899 from the Ryukyu Islands in the subtropical climate which is the same as that of the Bonin Islands. After that it has widely extended its distribution. It invaded grasslands, felled sites, rocky cliffs, etc. and occupied the vacant niche of the pioneer tree stage in secondary succession (NUMATA and OHSAWA 1970, SHIMIZU and TABATA 1985). Indigeneous evergreen broad-leaved tree, *Schima mertensiana* follows the pine stage which becomes stable, as shown in Table 1 (NUMATA and OHSAWA 1970). This is an example of secondary succession including the introduced *Pinus lutchuensis* on the humid site of *Schima mertensiana* type mountain forest in Chichijima (Father Island). In these cases, the floristic composition and reproductive structure of the *Schima* forest is shown under the canopy of *Pinus lutchuensis*.

In Japanese lowlands, there are *Pinus densiflora* and *P. thunbergii* on Honshu, Shikoku and Kyushu, and *P. lutchuensis* in the Ryukyu Islands. After the war, many pine stands are widely infested with a nematode disease carried by a longhorned beetle. The disease invaded Chichijima in 1979, and 80% of the adult trees (260,000)died. However, seedlings and saplings have been not infested (SHIMIZU 1987).

Table 1. One example of *Pinus lutchuensis* forest in the Bonin Islands (Chichijima).

| Layer | Species | SDR |
|---|---|---|
| 1 (18~15m) | *Pinus lutchuensis* | 100 |
| | *Schima mertensiana* | 80 |
| 2 (5 m) | *Trachelospermum foetidum* | 100 |
| | *Rhaphiolepis wrightiana* | 60 |
| 3 (2.5~2m) | *Schima mertensiana* | 90 |
| | *Callicarpa glabra* | 60 |
| | *Machilus kobu* | 50 |
| | *Ardisia sieboldii* | 50 |
| | *Morinda boninensis* | 50 |
| 4 (< 1 m) | *Carex hattoriana* | 75 |
| | *Thelypteris parasitica* | 70 |
| | *Pandanus boninensis* | 52 |
| | *Ctenitis lepigera* | 32 |
| | *Syzygium buxifolium* | 27 |
| | *Ligustrum micaranthum* | 27 |
| | *Psychotria boninensis* | 27 |
| | *Trachelospermum foetidum* | 23 |
| | *Ardisia sieboldii* | 17 |
| | *Fagara boninensis* | 17 |

## Casuarina equisetifolia

*Casuarina equisetifolia* was introduced to the Bonin Islands from Australia in 1879. It was planted along the sea-coast as a windbreak, however it invaded eroded red soil of inland areas. *Casuarira equisetifolia* is used in general for coastal forest in the tropical and subtropical regions. An example of a coastal forest is shown in Table 2 (NUMATA and OHSAWA 1970). At an air-field abandoned during the war, *Casuarina equisetifolia* is 3m in height and covers 35% of the area. *Leucaena leucocephala*, *Paspalum conjugatum*, *Cynodon dactlon*, *Erigeron floribundus*, and *Chloris radiata* are scattered in disribution there. Such an inland open space is occupied by many alien plants, among which *Casuarina equisetifloia* is a leading species. *C. equisetifolia* forest belt along the sea coast is established well and looks indigeneous.

Table 2. A coastal forest of *Casuarina equisetifolia* in the Bonin Islands

| Layer | Species | SDR |
|---|---|---|
| 1 (18m) | *Casuarina equisetifolia* | 100 |
| | *Desmanthus virgatus* | 100 |
| 2 (2～1 m) | *Leucaena leucocephala* | 75 |
| | *Cyperus alternifolius* var. *obtusangulus* | 75 |
| 3 (<0.5m) | *Cynodon dactylon* | 88 |
| | *Chloris radiata* | 75 |
| | *Digitaria pruriens* | 51 |
| | *Rhaphiolepis umbellata* | 51 |
| | *Paspalum dilatatum* | 39 |
| | *Tetragonia tetragonoides* | 24 |

## Leucaena leucocephala

*Leucaena leucocephala* is frequently seen in South Pacific Islands. *L. leucocephala* was introduced from India in 1879, and its community covers a large area in the Bonin Islands. It easily invades forest-destroyed sites. At an abandoned air-field, there was *L. leucocephala* scrub (Table 3, NUMATA and OHSAWA 1970). However, it usually occupies the margin of natural forests, therefore when we walk on a path, we sometimes have an illusion that all parts of forest are covered by *L. leucocephala*. One example of a marginal

Table. 3. *Leucaena leucocephala* scrub at an abandoned air-field in the Bonin Islands

| Species | SDR |
|---|---|
| *Leucaena leucocephala* | 100 |
| *Paspalum conjugatum* | 75 |
| *Vitex rotundifolia* | 58 |
| *Stachytarpheta jamaicensis* | 51 |
| *Digitaria pruriens* | 41 |
| *Cynodon dactylon* | 18 |
| *Cyperus polystachys* | 13 |

*L. leucocephala* forest is shown in Table 4 (NUMATA and OHSAWA 1970). Sometimes, the *Scaevola sericea* belt along the sea coast is occupied by *L. leucocephala*. Its density is very high, and the relative light intensity is very low (less than 5% at 1m high under the canopy. The highest stand was 10m high, and basal area was 0.3%, along with as a lower one (Table 4). An alien animal, the African snail, was concentrated in the *L. leucocephala* belt around the natural forest.

Table 4. *Leucaena leucocephala* forest at Kiyose in Chichijima, the Bonin Islands.
The coverage of the 2nd layer was 3%.

| Layer | Species | SDR |
|---|---|---|
| 1 (4.5~1.5m) | *Leucaena leucocephala* | 100 |
| | *Desmanthus virgatus* | 48 |
| | *Cyperus alternifolius* var. *obtusangulus* | 25 |
| 2 (< 1 m) | *Stachytarpheta jamaicensis* | 100 |
| | *Cyperus compressus* | 25 |
| | *Desmanthus virgatus* | 20 |

There was a workshop on the *Leucaene* Research in the Asian-Pacific Region organized by the Netrogen Fixing Tree Association and International Development Research Centre (1982) an abstract from which says that because of *Leucaena leucocephala*'s multiple uses as forage, fuelwood, poles, green manure, etc., this fast-growing, nitrogen fixing tree has been subject of much research in the last decade. However, in our case, the tree is harmful for the nature conservation of indigeneous vegetation.

In the Ryukyu Islands, there was a similar infestation of introduced *Leucaena* which was recently damaged by a noxious insect (*Heteropsylla cubana*, jumping plant lice) (SAKAGUCHI 1987). After the defoliation caused by the insect, a climbing plant, *Ipomoea indica* rapidly ascended and is now growing thickly (MIYAGI 1987). We observed a similar phenomenon after the death of bamboo (NUMATA and AOKI 1962).

## Alien grasses and herbs in semi-natural stands

The phenomena of the invasion of and occupation by alien grasses and herbs, such as

*Ambrosia artemisiifolia*, *Erigeron annuus*, *Solidago altissima*, etc. in semi-natural stands is seen frequently throughout the world. We conducted denuded quadrat experiments to verify the successional sequence of alien species in the pioneer stages (NUMATA and YAMAI 1955). After that, we clarified the causes of their prosperity as being due to allelopathy (NUMATA 1978, 1982). One of them, the *Erigeron floribundus* grassland is shown as a grassland type in Japan (NUMATA 1969－Table 5). In it, we can see alien herbs such as *Erigeron sumatrensis*, *E. annuus*, *E. canadensis*, and *Trifolium repens*, and alien grasses such as *Dactylis glomerata*. These are also found in roadside fragmental vegetation.

Table 5. Floristic composition of an *Erigeron* type grassland

| Species | SDR |
|---|---|
| *Erigeron floribundus* | 88 |
| *Artemisa vulgaris* var. *indica* | 65 |
| *Erigeron annuus* | 55 |
| *Erigeron canadensis* | 45 |
| *Dactylis glomerata* | 35 |
| *Rhus javanica* | 34 |
| *Agrostis palustris* | 33 |
| *Miscanthus sinensis* | 27 |
| *Rubus crataegifolius* | 26 |
| *Setaria viridis* | 25 |
| *Siegesbeckia pubescens* | 10 |
| *Trifolium repens* | 9 |
| *Cassia mimosoides* var. *nomame* | 8 |
| *Hypericum erectum* | 6 |

I studied the floristic change of the same coastal vegetation on the Futtsu Cape, Chiba Prefecture (NUMATA 1949, MITSUDERA and NUMATA 1964). In the former there was an ecotonal community between two coastal communities of the northern bayshore and southern open seashore which included *Erigeron floribundus*, *Oenothera erythrosepara*, and *O. stricta* as well as *Carex kobomugi*, *Imperata cylindrica* var. *koenigii*, *Zoysia macostachya*, *Fimbrystylis sericea*, and *Calystegia soldanella*. However, *Oenothera erythrosepara* and *O. stricta* was completely replaced by *O. laciniata* in 1964. This is a kind of displacement naturalization of earlier aliens by a new alien, and not the displacement of indigeneous species by an alien.Therefore, we can say that there are two types of

relationships involving aliens, indigeneous vs. alien, and alien vs. alien displacement.

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