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PHOSPHATE MINING INDUCED VEGETATION CHANGES ON NAURU ISLAND[1]

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Abstract. Postmining succession and pre-mining forest vegetation were studied on the isolated, tropical, central-Pacific, phosphate-rich island of Nauru. An analysis was made of the extent to which natural vegetation has been reestablished on the highly disturbed open-pit phosphate-mined areas that constitute some three-quarters of this 22-km^2 island. Sixty-four sample quadrats were taken from the successional range of revegetated mined areas and from the unmined plateau forest. Frequency and percent cover were obtained for all species to determine their ability to colonize different microhabitats in the mined area. A complete inventory was also made of all plant species present on Nauru, to identify the pool of potential recolonizers of the mined area.

Of the 467 plant species found on Nauru, 47 native and 79 introduced weed species are potential short- and long-term colonizers. We found 50 of these 126 potential colonizers in the 64 sample quadrats. Highly dispersible, exotic weed species predominate in primary succession, but they are rapidly replaced by native plants such as *Dodonea viscosa* and *Ficus prolixa,* and by pantropical strand plants such as *Scaevola taccada, Morinda citrifolia, Premna obtusifolia, Guettarda speciosa,* and *Calophyllum inophyllum.* These species are scattered and stunted, however, when compared to their growth habit in the unmined forest. The resultant succession seems to be progressing very slowly in the highly disturbed habitats. Centuries will be needed for the forest to reestablish naturally, even in a modified form, and most likely the forest will be composed primarily of *Calophyllum inophyllum* and other native coastal strand trees as dominants, with *Ficus prolixa* on the exposed coral-limestone pinnacles that remain after mining. If, however, the landscape is artificially modified by leveling the pinnacles and filling in the pit bottoms, and if suitable exotics are introduced, the succession could be altered considerably, much to the benefit of postmining generations of Nauruans.

Key words: degradation; disturbance; ecology; island; mining; Nauru; Pacific; phosphate; plagioclimax; revegetation; strand; succession.

INTRODUCTION

More than 70 yr of opencut phosphate mining has severely modified the vegetation and environment of the small, isolated, tropical Pacific island of Nauru. This history of human disturbance, coupled with the introduction of exotic plant species in the absence of quarantine regulations, provides an excellent opportunity to examine the susceptibility or vulnerability of the indigenous island flora to degradation or extinction, the competitive abilities of native and exotic species during successional stages, the ecological adaptability of ubiquitous strand species, and the postmining potential natural vegetation of Nauru.

BACKGROUND

The uniqueness and fragility of Pacific island ecosystems and their natural vegetation have long attracted the attention of scientists, including such recent workers as Fosberg (1965), Mangenot (1965), Dorst (1972), Mueller-Dombois (1975), and Carlquist (1980). Dasmann et al. (1973:48) stressed the disastrous effects and almost total disruption of island ecosystems that have resulted from inappropriate development projects and land use.

One aspect of this disruption that has received particular attention is the role of humans in habitat modification and plant dispersal (Darwin 1859, Hooker 1867, Wallace 1880, Harris 1962, Fosberg 1965, Thaman 1974). Mangenot (1965:121–122), for example, stressed that the transformation of natural forest microclimates into new microclimates with increased sunlight and lower humidity, coupled with the diffusion of plant propagules, has been responsible for "opening to numerous species new areas from which they were formerly barred." Furthermore, when more aggressive plants of continental origin have been introduced, they have commonly spread rapidly, displacing the native species, which had evolved in relative isolation (Dasmann et al. 1973, Carlquist 1980).

It is widely believed that, as a consequence, exotics will permanently dominate restabilized vegetation on Pacific islands. Studies by Egler (1942) in Hawaii and Harris (1962) on three West Indian islands have shown, however, that although aliens may become dominant through human influence, they are unlikely to maintain this dominance if human interference is later excluded. Similarly, in Hawaii, Mueller-Dombois (1975:364) observed that although sweeping invasions of exotics may

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occur in poorly occupied niches, most exotics do not penetrate into established communities unless new niches are created by direct disturbance.

The vulnerability of native island floras seems to be primarily due to the fact that they have evolved in the relative absence of competition (Darwin 1859, Carlquist 1965, 1980, Mueller-Dombois 1975). Island ecology differs from continental ecology, especially at the level of species interaction. On islands, only a few, well-adapted species may exist in certain life-form groups; their amplitude can be unusually broad because of the absence of competitors, and there is commonly a high degree of endemism (Mueller-Dombois 1975). However, in comparison with floras of the larger, higher islands like the Hawaiian or Fijian archipelagos, the floras of smaller, low-lying atolls and coral-limestone islands such as Nauru are generally poorer, have a low degree of endemism, and are composed primarily of plants adapted for survival in habitats subject to storm waves, salt spray, and tidal flooding. Although these coastal plants are ubiquitous on Pacific island coasts and have primarily a cosmopolitan or pantropical distribution, they have been shown to have very narrow ecological tolerances; they often grow "in a file along the shore only one or a few plants wide" (Sauer 1976:2), and thus would seem particularly susceptible to displacement or extinction as a result of habitat destruction.

Evidence as to which seral developments will take place in disturbed habitats, or what the end point of succession will be, varies from study to study. Küchler (1964) stressed that because of the considerable, long-term, often irreversible impact of humans on the environment, it is very difficult to know what the post-disturbance vegetation might be anywhere, let alone on Nauru. A classic study is that of the revegetation of the Indonesian volcanic island of Krakatoa. The violent eruption on that island in 1883 provided a completely sterilized environment where "Not a tree, shrub or other plant survived" (Went 1949:137). Although all life forms were killed and covered with a layer of ash up to 30 m in thickness, "only 50 years later, a rich and maturing tropical rainforest with over 250 component species and many epiphytes had re-established itself . . ." (Watts 1971:258). The recovery of native plants after volcanic eruptions has also been studied for a 9-yr period in Hawaii (Smathers and Mueller-Dombois 1972, Mueller-Dombois 1975). These studies indicated that native pioneer species are better adapted to the new, edaphically extreme habitats, but that exotic species participate in primary succession.

Palaniappan's (1974) comparisons of the species composition of surrounding secondary forests with that of the tailings forest in West Malasia indicated that "it is possible for a tailings forest to reach that stage of a true, natural, and matured secondary forest with more or less the same species composition." He found that, although the highly disturbed tailings habitat was "unique and unusual," the vegetation that colonized it was "not particularly so" (Palaniappan 1974:149–150).

We have attempted in the present study to discover whether some of these previous findings apply to the smaller, isolated, coral-limestone island of Nauru. In short, we examined the extent of postmining recovery of vegetation, the relative dominance of native and exotic species at different stages of succession, and the ecological tolerances of the ubiquitous strand species.

Study Area

Nauru is a small, isolated, uplifted, coral-limestone island located 42 km south of the equator at 166°56′E, and lying ≈4000 km north of Sydney, Australia, and 4160 km west of Honolulu, Hawaii (Fig. 1). It is an independent republic with an estimated population of 7700 people as of March 1979, of whom 4600 are Nauruans of somewhat mixed but primarily Micronesian origin. The balance includes I Kiribati and Tuvaluans (Gilbert and Ellice Islanders from the former British colony), Solomon Islanders, Chinese, Filipinos and Europeans, all of whom are contract workers for the Nauru Phosphate Corporation (NPC), and another 400–500 expatriates working either for the Nauru government or for NPC (Carter 1981).

The island itself is only 22 km^2 (2200 ha) in area. The coastal plain ("bottomside") encircling the island ranges from 150 to 300 m wide. From the inner border of this coastal plain, a coral-limestone escarpment rises to a central plateau ("topside") ≈30 m above sea level. The central portions of the escarpment are composed largely of rock that bears high-grade tricalcium diphosphate [$Ca_3(PO_4)_2$]. The highest point on the island is 70 m. The natural vegetation of the plateau was "tomano" (*Calophyllum inophyllum*) forest. The annual precipitation is extremely variable; the mean is 203 mm/yr and the range is 104–4572 mm/yr (Carter 1981). Laboratory analyses indicated that the soils of the coastal strand and the plateau forest have low water-holding capacities and an alkaline reaction.

Cultivation is restricted almost exclusively to the coastal belt and to the area surrounding Buada Lagoon, where coconuts, *Pandanus* and some breadfruit, mango, soursop, and other fruit trees are found. Bananas, some vegetables, and other food crops are grown by I Kiribati, Tuvaluan, Chinese, and Filipino indentured workers at Location (the indentured-worker settlement) on the coastal belt, in the swampy areas bordering Buada Lagoon, and near the Topside Workshops. In the past, Nauruans purposely planted *Pandanus* groves on the plateau, of which remnant stands can still be found.

Near the beginning of this century, Nauru was discovered to have very extensive deposits of tricalcium diphosphate rock that were the second richest in the world (the richest were on neighboring Ocean Island).

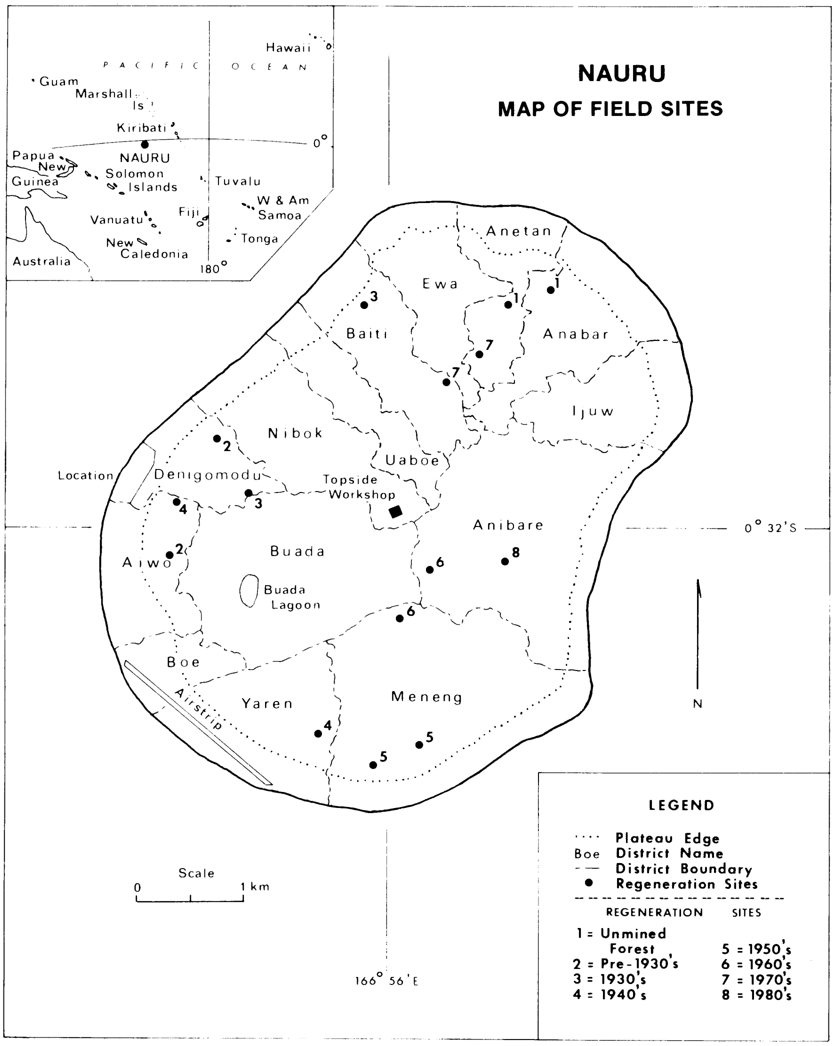

FIG. 1. Location map of Nauru and field sites. A total of four sample quadrats were analyzed within each of the two "regeneration sites" designated 1 to 7, and 8 from the site designated 8 (yielding the total of 64 sample quadrats).

The rock contained 38.9% phosphorus pentoxide and had few impurities (Tyrer 1968, Viviani 1970). Except for interruptions during World War I, and again during World War II, these deposits have been mined continuously since 1906. The industry can now produce in excess of 2 million Mg/yr, most of which is destined for Australia and New Zealand (Kelly 1977:4).

Phosphate mining on Nauru involves the removal of the vegetation, the topsoil, and contaminated phosphate to expose the purer phosphate deposits. Trees and other plant refuse are transported to a dump, where they are burned, and the topsoil and contaminated phosphate are stockpiled by the mining company for future use. The topsoil and contaminated phosphate are not replaced after mining. Since the phosphate is normally found between coral-limestone pinnacles, its extraction by 0.48- and 0.76-m^3 Ruston Bucyrus power "grab buckets" results in a dramatic change in local relief. This generally varies between 4 and 8 m from the top of the exposed pinnacles to the pit bottoms. Although the area covered by pinnacles is quite variable, about three or four pinnacles were found within each of our 100-m^2 quadrats. Owing to the inefficiency of the mining process, up to 20% of the phosphate remains after extraction (G. Bailey, *personal communication*), forming loose deposits in the pit bottoms and on saddles and scree slopes between and against pinnacles. These provide the main sites for recolonization and revegetation. Further sites for recolonization include cracks in the surfaces of the pinnacles.

In general, phosphate mining removes the original vegetation and soil completely, leaving only small, raised, rocky outcrops or "islands," which are currently unminable. The development of a new plant community on the mined surfaces may therefore be considered a primary succession on a new substrate that was the result of catastrophic intervention by humans.

Around the year 2000, the phosphate deposits will be exhausted, and an estimated four-fifths of the total land area or 1760 ha will have been transformed into pitted, barren wastelands with scattered coral pinnacles, which have been described as "soil-less craggy lunarscapes" (Hawkins 1981:19). The >70 yr of open-cut phosphate mining, coupled with virtually no attempt whatsoever to rehabilitate, had left by 1981 a severe and highly disturbed habitat for plant recolonization. Although this habitat has a limited potential for future human utility, it does provide a unique laboratory for testing some of the hypotheses and observations about the ecology of Pacific islands cited earlier.

Field Methods

Field work on Nauru was conducted during 2-wk periods in November 1980 and July 1981. During these periods, reconnaissance vegetation surveys were made of the entire island. Sample quadrats were located in all distinctive natural and cultural vegetation associations. All plant species, subspecies, and varieties were recorded, and, where possible, specimens were collected.

For the study of vegetation regeneration after phosphate mining on the plateau, records of the Nauru Phosphate Corporation were examined, and the time period of mining in each leased area was marked on a map with a scale of 1:7920. Mined areas were then grouped into "mining decades." Since records of mining activities prior to 1930 were incomplete or unavailable, these years were grouped into a single decade termed "Pre-1930." The resultant sampling scheme, including the period of 1980 to the present, consisted of seven mining decades.

In the unmined areas, the topography was flat or gently undulating; there were occasional rock outcrops or "islands" and exposed coral-limestone pinnacles. The soil surface was often littered with coral-limestone rubble and old cans, bottles, and other trash. In the mined sites, however, the very broken topography of pits and pinnacles made it necessary to distinguish three microhabitat types, and to assess the relative abundance in each of these, for all the species sampled. These microhabitat types were: (1) bare-rock surface (usually the exposed tops and sides of pinnacles), (2) relatively unstable scree slopes and saddles caused by the inefficient mining process or by weathering, and (3) pit bottoms or floors.

Eight sample quadrats (10 × 10 m) were located randomly within "typical" unmined forest areas and within each mining decade, but well away from the edge effects produced by roads and adjacent vegetation. Although most of the quadrats in the unmined areas had been subjected to some degree of disturbance, the canopy trees did not seem to have been greatly affected. Hence, these forests were used as examples of the climax vegetation or "potential natural vegetation" that existed prior to mining, and to which the mined areas might be expected ultimately to return. We assumed that there had been a relatively uniform pre-mining plateau environment similar to the remaining unmined areas.

Values of cover abundance were recorded for all species in each of the 64 quadrats by using a modified Braun-Blanquet scale, as follows:

Cover class	Midpoint of cover-class (%)
5 = cover >75%	87.5
4 = cover 50–75%	62.5
3 = cover 25–50%	37.5
2 = cover 10–25%	17.5
1 = cover 5–10%	7.5
+ = cover <5%	2.5

In the mined sites, these values were recorded for each microhabitat. Each value in the cover scale was assigned the midpoint cover value for that cover-class, and for each species these cover values were averaged, within each of the three microhabitats, over the eight quadrats. These mean cover values for each of the three microhabitats were then summed and divided by three to yield an average percent cover for that species at that site. Number of occurrences was also calculated for all recorded species in the 64 quadrats.

Results and Discussion

The frequencies of occurrence and the mean percentage cover for each species found in the 64 sample quadrats are presented in the Appendix. The Appendix also includes the percentage cover and the frequencies of occurrence of each species in the mined sites according to habitat (scree slopes, pit bottoms, or rock pinnacles).

The mean cover percentages for species occurring in at least four quadrats are presented graphically in Fig. 2. These graphs illustrate the competitive roles of indigenous and exotic plant species during the course of succession.

Original plateau forest

In mid-1981, an estimated 12–15%, or 200–250 ha, of the pre-mining forest either remained to be mined or was unminable. While our observations of the unmined forest were restricted to only a small portion of the plateau, the small size of the island and its climatic and topographic homogeneity indicate that the original vegetation on the plateau was probably quite uniform over its entire area. Information from Nauruans supports this assumption.

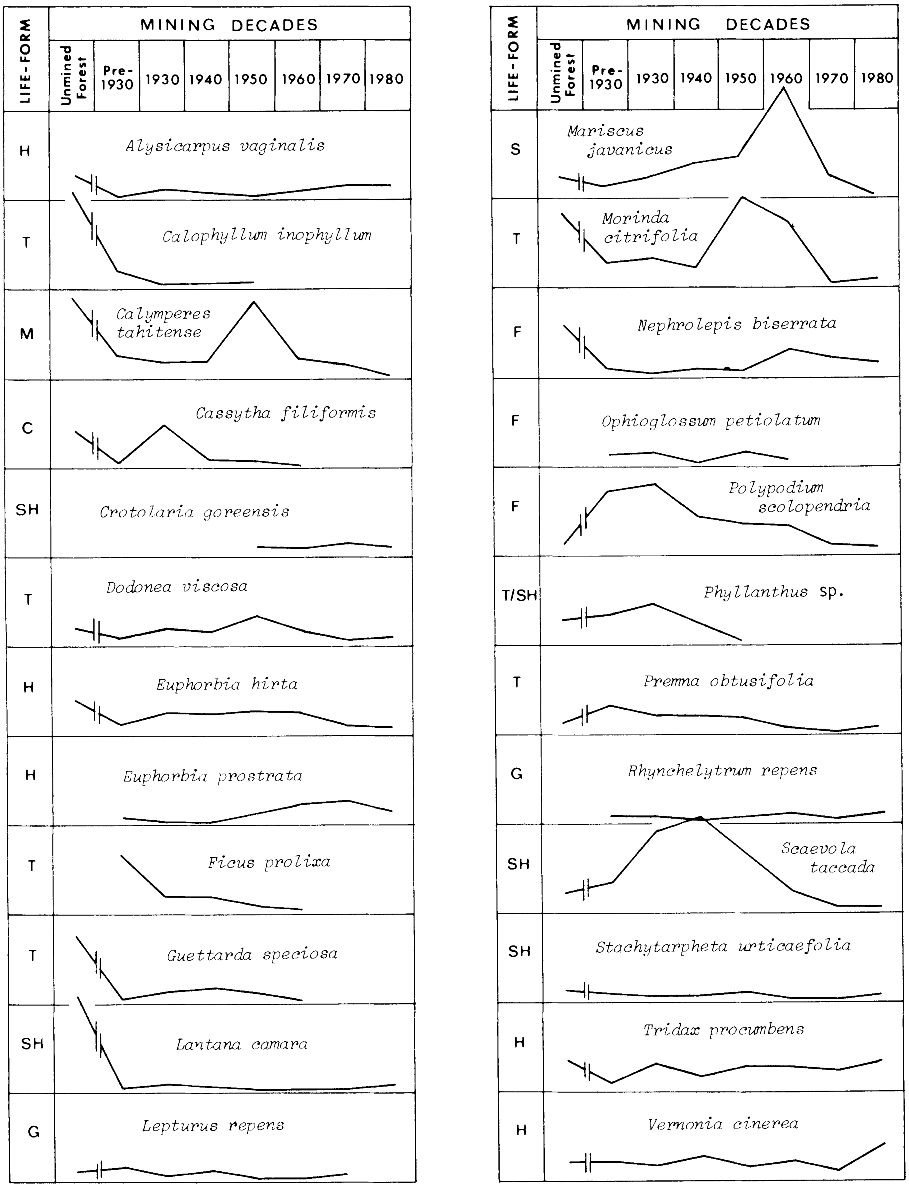

FIG. 2. Trends of mean cover percentage for species occurring in at least four study sites. Vertical scale varies: *Calophyllum inophyllum*, 0–60%; *Premna obtusifolia, Polypodium scolopendria, Scaevola taccada,* and *Lantana camara,* 0–16%; all other species, 0–4%. Key to symbols: C = creeper; F = fern; G = grass; H = herb; M = moss; S = sedge; SH = shrub; T = tree; T/SH = tree/shrub.

In a general survey of the vegetation of Nauru (H. I. Manner, *personal observation*) two main indigenous forest types were recognized on the plateau. The first of these is dominated by *Ficus prolixa* and is similar to that found along the escarpment or transition zone between the coastal plain and the plateau. On the plateau, it is found primarily on rocky outcrops, hill crests, or other exposed areas where the phosphate and topsoil have been eroded from between the pinnacles. The resultant forest, with a canopy of 12–20 m, is dominated by *F. prolixa,* which has a relative importance value of between 45 and 95% (calculated from estimates of basal area). Characteristic secondary canopy species include *Terminalia catappa, Pisonia grandis, Ochrosia elliptica,* and *Guettarda speciosa.*

The second forest type, which would have covered >90% of the plateau, is dominated almost entirely by *Calophyllum inophyllum* (relative importance value of between 95 and 100%). It is the most highly stocked forest of those sampled, with basal areas up to 129 m^2/ha, and has an average canopy height of 16 m. *Guettarda speciosa, Morinda citrifolia,* and the introduced *Psidium guajava* are infrequent components among the canopy species. Small stands of *Pandanus* are also found on the plateau, especially near the escarpment. In the past, these commonly were planted for their fruits, which are a traditional staple and snack food. The topsoil in this forest is continuous; exposed pinnacles, usually occupied by solitary *F. prolixa,* are uncommon.

The eight (10 × 10 m) sample quadrats of unmined areas that were used for comparison with the vegetation on the seven mining decades were located in the second forest type. The results were consistent with those of the general survey: *Calophyllum inophyllum* was the dominant canopy species in all sample quadrats. Rare (canopy) trees in the samples included *Guettarda speciosa* and *Premna obtusifolia.* In the subdominant stratum, the almost ubiquitous presence of the introduced *Lantana camara* and to a lesser extent *Psidium guajava,* indicated either that the understory was quite disturbed or that these species successfully competed with the native species. Other introduced species found in at least 50% of the quadrats included *Chrysopogon aciculatus, Euphorbia hirta, Tridax procumbens,* and *Desmodium triflorum.* These four are all small, herbaceous species and are not a weed problem. *Lantana camara,* however, is a very vigorous shrubby species that impairs regeneration on several other Pacific islands and in Australia (Thaman 1974). In Nauru, it seemed to be naturally restricted when under the canopy of *C. inophyllum.* Among the indigenous species in the unmined forest, the parasitic climber *Cassytha filiformis* was frequently encountered, but was not as abundant as on the coastal plain. *Psilotum nudum* was also common in unmined areas. This species appeared to prefer a habitat in the shade, at the base of *C. inophyllum* or under *Scaevola taccada. Morinda citrifolia* and *S. taccada* were frequent in the shrub layer, and the pteridophytes *Polypodium scolopendria* and *Nephrolepis biserrata* commonly formed patches under *C. inophyllum.* They also occurred as sciophytic bole climbers. *Calymperes tahitense* abounded on exposed roots and scattered coral-limestone rubble on the soil surface.

This description is adequate for the main forest type that may have covered much of the plateau prior to mining. Other, rarer species may once have been widespread or locally abundant in patches or clumps, but only the most common species are mentioned here. Nauru has been inhabited for unknown centuries, possibly for over two millennia, and the plateau forest has undoubtedly been disturbed by hunting, gathering, and other activities. Consequently, it is not really possible, in the absence of palynological evidence, to deduce any changes in species composition.

The first 40 yr of succession

Studies of the most recently mined areas showed that the first pioneer species arrived within months of the completion of mining in a particular area. The easily dispersible species such as *Vernonia cinerea* and *Tridax procumbens* were initially prominent, and were most common on the scree slopes and pit bottoms. They also occurred on the more exposed pinnacle surfaces. The well-dispersed pteridophytes *Polypodium scolopendria* and *Nephrolepis biserrata* were also prominent in the very early stages. They grew mainly on the shady sides and near the bases of pinnacles. The rhizomes of these two ferns were equally capable of colonizing the cracked surfaces of pinnacles and the friable phosphate remains of the scree slopes and pit bottoms. Furthermore, *Euphorbia prostrata, Crotolaria goreensis,* and *Cleome rhytidosperma* were also found on very recently mined sites (mean frequencies of occurrence are three, three, and eight plants per eight quadrats, respectively). *E. prostrata* could utilize all three habitat types, and remained in the vegetation for some time, but *C. rhytidosperma* could not colonize the exposed, sunny pinnacles, and soon disappeared from the sequence. Such transient presence may also be typical of other rapidly dispersed species such as *Eragrostis tenella, Phyllanthus amarus, Euphorbia cyathophora, Hedyotis corymbosa,* and *Synedrella nodiflora,* all of which are widespread tropical ruderals that are quick to colonize open habitats, but are unable to sustain their populations against competition from larger, more long-lived, shade-producing species.

Mariscus javanicus was not recorded from the most recently mined areas. Its peak of abundance was in the 20-yr-old sites, where it was the most frequent species and had the highest cover percentage, followed closely by *Polypodium scolopendria* and *Nephrolepis biserrata.* With increasing plot age, *M. javanicus* became progressively less abundant as its preferred habitat became increasingly shaded and crowded with other species.

With the exception of the two pteridophyte species, all species with high frequencies and mean cover values in the recently mined sites have been introduced by humans, and all are herbs or forbs. Most seem to be recent (post–World War II) introductions, although *M. javanicus* is thought to be an aboriginal introduction. Whatever their origins, it is clear that these herbaceous exotic weeds are most important in the first stages of postmining succession.

The four species with cover maxima in the 20–40 yr old sites were *Scaevola taccada, Morinda citrifolia, Dodonea viscosa, Fimbristylis cymosa,* and *Calymperes tahitense.* All except *F. cymosa* were also present in the newly mined areas and represented the first indigenous colonizers. *C. tahitense,* which attained a maximum cover in the 30-yr-old sites, was particularly able to colonize shady parts of the bare-rock surface, as well as the scree slopes, and probably fulfilled an important role in soil formation. Moreover, it persisted in the older areas and was quite common on the scattered rocks and boulders in the unmined forest. *F. cymosa* had a somewhat patchy, clumped distribution in the plots, and had cover peaks in both 40- and 60-yr-old sites. It was abundant in ruderal communities on the coastal plain, and in the mined areas it was most common in the pit bottoms. It could also colonize scree slopes and cracks in bare rock. *F. cymosa* was rarer on sites older than 60 yr and was not recorded in the unmined forest.

Scaevola taccada and *D. viscosa,* both pioneer woody species, represented the first nanophanerophytes to appear in the revegetation sequence. They preferentially colonized the pit bottoms and scree slopes, but also became established on pinnacles, where they rooted in rock cracks and produced stunted individuals. *D. viscosa* had a clear maximum cover and frequency on 30-yr-old sites. It also occurred as a ruderal plant on both the plateau and the coastal plain, but was rare or absent in the coastal strand and unmined forest. *S. taccada* had a pronounced maximum cover on 40-yr-old sites. Its abundance and dominance decreased on older sites, but its frequency was maintained. In contrast with *D. viscosa, S. taccada* was common throughout Nauru. It was one of the most abundant species of the strand flora and was an excellent colonizer of the mined areas. It may be useful in other tropical or subtropical situations as a rehabilitator of coastal areas after mining. In general, it dominated the canopy of the 20–40 yr old sites, and characterized the second stage in revegetation of the mined areas.

This second stage also contained examples of locally successful colonization of mined areas by *Casuarina litorea* and *Muntingia calabura,* both of which are introduced tree species on Nauru. Both species seem to have been dependent on seed-source proximity. The very dense local concentrations of *Casuarina litorea* on mined areas can be attributed to dispersal from plantings around the nearby Topside Workshops. The very dense stands of *Muntingia calabura* found over an area of ≈2 ha in the interior of Ewa district could possibly be attributed to dispersal of its sweet, red berries by birds. Although *M. calabura* was not present in the study sites, both species seem to be successful colonizers in these harsh conditions. In fact, *Casuarina litorea,* a dominant on severe, rocky coasts throughout the Pacific, was the first tree to colonize Krakatoa (Went 1949), and has become naturalized in the Florida Everglades (Egler 1952) and in Mauritius (Sauer 1961, 1976).

In summary, the first 40 yr consisted of two main intergrading vegetation phases. The first was the initial, rapid colonization by introduced herbaceous weeds. In the second stage, the introduced herbaceous weeds were replaced primarily by indigenous woody shrubs. These latter plants are more long lived, and produced a canopy that probably encouraged the growth of more shade-tolerant species, especially in the pit bottoms and on lower scree slopes.

The second 40 yr of succession and beyond

The division of the successional lands into the first 40 yr (areas mined after World War II), and the second 40 yr (areas mined prior to 1940) is somewhat arbitrary. Given this division, however, the sampling data clearly show a set of six species (*Ficus prolixa, Premna obtusifolia, Phyllanthus* sp., *Ophioglossum petiolatum, Polypodium scolopendria,* and *Cassytha filiformis*) with cover maxima in 40–60 yr old sites, and which are all considered to be indigenous to Nauru. Although each had its cover maximum in this age range, the individual graphs were quite different, which reflects differences in the species' colonizing ability and in their ultimate fate in the composition of the climax vegetation.

The herbaceous fern *Polypodium scolopendria,* which colonized all three habitats, was also the most frequently encountered species on the regenerating sites (Appendix). Unlike *Scaevola taccada, P. scolopendria* is rare on the coastal plain and strand of Nauru. However, it was present in six of the eight 0–10 yr old sites, thus showing its rapid colonization potential. It was observed in 92% of all sample sites. *P. scolopendria* gradually covered more and more area and reached a maximum in the 40–60 yr old sites. In the pre-mining plateau forest, *Polypodium scolopendria* was an important component of the ground layer.

The 1–1.5 m, shrubby *Phyllanthus* was first observed in the succession sequence in the 30–40 yr old sites, where it was found in four of eight quadrats. Its cover abundance and frequency clearly peaked in the 40–50 yr old sites. This *Phyllanthus* species colonized all three habitat types, but apparently it was unable to persist, perhaps because of competition from much taller and more vigorous species.

Two other species in this group of late-successional natives are trees: *Premna obtusifolia* and *Ficus prolixa. Premna obtusifolia* was first observed in the 0–10 yr old sites, while *Ficus prolixa* was found in the 1950 mining sites. Both of these species were capable of colonizing the rock surface of the pinnacles just as well as, if not better than, the more mesic scree slopes and pit bottoms. Growth in the mined areas seemed slow, and even after 60 yr of vegetation development, the canopy attained only 4–6 m, compared with 16–20 m in the unmined forest.

Although *C. inophyllum* and *Guettarda speciosa* were found to grow in the older pit-bottom habitats, near unmined areas with many seed trees, they did not seem to be able to colonize the rock surfaces of the pinnacles as could *Ficus prolixa.* It would presumably take many thousands of years of erosion to modify the "pit and pinnacle relief" to its former, gently undulating surface. Only then would the original members of the pre-mining plateau forest (e.g., *C. inophyllum* and *G. speciosa,* and other secondary canopy species such as *Terminalia catappa, Pisonia grandis,* and *Ochrosia elliptica*) gain a competitive advantage. Thus the drastic changes in local topography and soil removal may be dominant factors leading to the development of a plateau plagioclimax community or "potential natural vegetation" quite different from what existed prior to opencut min-

TABLE 1. Distribution of plant species in study sites according to utility.

	Number of species	Un-mined forest	Mining decade Pre-1930	1930	1940	1950	1960	1970	1980	Totals
Exotic weeds	79	15	7	9	10	9	10	17	14	30
Indigenous species and/or aboriginal introductions	50	14	17	14	17	13	10	6	6	20
Total	467*	29	24	23	27	22	20	23	20	50

* The total number of Nauruan plant species includes 261 ornamentals and 80 food plants. None of these was found in the study sites.

ing. One must expect only a very slow change from a *Ficus prolixa*-dominated forest to a plagioclimax community dominated by *Calophyllum inophyllum* in the later stages of succession.

Exotic vs. native species

Since the discovery and initial settlement of the island, the Nauruan flora has been greatly expanded through the introduction of plant species. Tentative results (pending identifications) indicate that there are a total of 467 species of vascular plants on Nauru, belonging to 93 families. Forty-five species are considered to be indigenous, two either are indigenous or of aboriginal introduction, and three are aboriginal introductions. Seven species are considered to have been introduced by either aborigines or early Europeans, whereas 410 species were introduced after European contact. Of these 467 species, 341 are cultivated as ornamentals or food plants. The species are further classified and summarized in Table 1.

A total of 50 plant species, of which 20 are indigenous, were found in the sample quadrats. Thus, despite the 467 species present on Nauru, the plant species that could be considered as potential short- and long-term colonizers of the opencut mined areas on the plateau, seemed to be restricted to the 47 native species and 79 exotic, primarily weedy, species. Only 30 exotic weeds, the majority of which are post-World War II introductions, were recorded in the sample quadrats, and the introduced ornamentals seemed to be restricted to home gardens. Except for the two most recent mining decades, indigenous species outnumbered exotics in the study sites.

A possible explanation for the absence of these weeds from older sites would be that they were comparatively recent introductions to Nauru and were not available for colonization when the sites were first disturbed. This, however, is probably not the reason for their absence, as their spread from the coastal plain has been facilitated over the past few decades by the increasing number of roads, the increasing traffic, and the use of mechanical aids in mining. The comparative absence of exotic weeds in the older mined sites is consistent with the hypothesis that, while alien species may become established in recently disturbed sites, most are unlikely to persist in the absence of disturbance.

Coastal plain species

Several native strand plants such as *Scaevola taccada, Morinda citrifolia, Premna obtusifolia, Guettarda speciosa,* and *Calophyllum inophyllum* were found to colonize and persist as important components of the new forests at distances of up to 2 km from the coast. Their presence in the harsh, nonstrand habitats of Nauru's postmining pit and pinnacle topography and in the pre-mined forest suggests a refutation of Sauer's (1976) narrow ecological range thesis. Their spread into these disturbed noncoastal habitats may be due to a combination of their high tolerance to extreme conditions, the similarity of these conditions to that of the strand, and the absence on Nauru of competitors that may have greater demands on habitat resources. On the other hand, the absence from plateau sites of several common coastal species such as *Hibiscus tiliaceus, Barringtonia asiatica,* and *Tournefortia argentea,* may reflect their inability to colonize the extreme edaphic and microclimatic habitats found there, or their lack of suitable dispersal mechanisms. Other coastal species such as *Hernandia nymphaefolia, Thespesia populnea,* and *Triumfetta procumbens* may be absent from the plateau because habitat modifications along the coast have reduced their numbers almost to the point of extinction, thus reducing their probability of seed dispersal.

CONCLUSIONS

The study on Nauru has revealed several trends relating to the differential ability of predominantly native strand species to compete with weedy exotics in this highly degraded, small-island environment.

First, despite the proportionately large numbers of exotic and often weedy species on Nauru, 20 of the 50 species found in the study sites were indigenous to Nauru. Relatively few exotics are found as long-term dominants in the pre-mining forest. Although exotic ruderals are the initial colonizers of abandoned mined sites, they are rapidly displaced by indigenous species. Thus, the study on Nauru supports the conclusions of Mueller-Dombois (1975) and Harris (1962) that exotic species are generally only transient participants in successions, whereas native species are better adapted to long-term survival if human disturbance is removed. Native species achieve structural (and perhaps ecological) dominance 30–50 yr after cessation of mining, and it seems that even on edaphically severe islands like Nauru, cessation of a disturbance will eventually result in the reestablishment of an indigenous vegetation, albeit one quite different from the pre-mining plateau forest.

Of the indigenous species participating in succession, most are ubiquitous pan-Pacific strand species. Their dominance in both the pre-mining plateau forest and the successional sequence, in contrast with Sauer (1976), suggests that these species have broad rather than narrow ecological tolerances and are not particularly susceptible to displacement or extinction as a result of habitat destruction. Alternatively, the ecological conditions of the postmining successional sites and the unmined forest may be comparable with those of the strand. There are, however, some indigenous strand species that are rare on the coastal plain today and that seem susceptible to habitat modification. Their absence from the study sites may reflect their lack of suitable dispersal mechanisms and/or narrow ecological tolerances.

Phosphate mining on Nauru has so drastically altered the topography of the former, gently undulating plateau surface that the structure of the resultant forest will undoubtedly differ from the pre-mining forest. We suggest that, instead of a forest dominated by *C. inophyllum,* with *Guettarda speciosa, Morinda citrifolia, Terminalia catappa,* and others as infrequent secondary canopy species, there will be a very slow succession toward a plagioclimatic forest composed primarily of native coastal strand trees, with *C. inophyllum* in the pit bottoms and *Ficus prolixa* on the exposed pinnacles. *Casuarina litorea* and *Muntingia calabura,* which are locally dominant and aggressive in some of the revegetated sites, could also become more widely distributed.

For the pre-mining forest to reestablish itself, even in a modified form, will almost certainly take centuries. Even then, the *Pandanus* groves and many of the more culturally valuable plants, formerly part of the pre-mining plateau forest, will be absent. The only alternative, if Nauruans hope to remain on this upraised coral-limestone island, is to use some of the capital derived from phosphate mining to artificially alter and accelerate the revegetation of the central plateau. This may be achieved through leveling and crushing the coral-limestone pinnacles, importing soil, and purposely planting appropriate indigenous and exotic species. In the event of such a program, it would, however, be of critical scientific and cultural importance to ensure that examples of unmined forest vegetation and pit and pinnacle topography are preserved for posterity.

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APPENDIX: see pages 1464–1465

APPENDIX

Frequency and mean cover for species in unmined and mined quadrats (eight quadrats per decade).

		Pre-1930				1930†				1940			
	Unmined forest	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.
Trees													
Calophyllum inophyllum	8/63.10*	4/20.00	1/7.81	···	4/9.27	···	···	···	···	1/0.31	···	···	1/0.10
Casuarina litorea	···	···	···	···	···	···	···	···	···	···	···	···	···
Dodonea viscosa	···	2/0.62	···	···	2/0.21	2/1.25	···	1/0.31	2/0.52	2/0.62	1/0.31	1/0.31	3/0.42
Ficus prolixa	···	1/0.94	···	7/5.94	8/2.29	···	···	4/1.88	4/0.62	···	···	6/1.88	6/0.62
Guettarda speciosa	2/1.87	···	···	···	···	···	1/0.94	···	1/0.31	2/0.62	1/0.94	···	3/0.52
Morinda citrifolia	6/3.10	2/0.62	1/0.31	4/1.88	6/0.94	5/1.56	3/0.94	2/0.62	8/1.04	···	1/0.31	4/1.88	5/0.73
Phyllanthus sp.	3/0.94	3/1.56	2/1.25	2/0.62	4/1.14	7/2.19	5/1.56	4/1.25	8/1.67	3/0.94	3/0.94	3/0.94	3/0.94
Premna obtusifolia	4/1.25	7/9.69	4/4.38	4/1.88	8/5.31	8/5.00	3/2.19	6/2.50	8/3.23	5/4.69	4/1.25	5/3.44	8/3.12
Psidium guajava	6/2.80	···	···	···	···	···	···	···	···	1/0.31	···	···	1/0.10
Terminalia catappa	1/0.31	1/4.69	···	···	1/1.56	···	···	···	···	···	···	···	···
Shrubs													
Colubrina asiatica	···	···	···	···	···	···	···	···	···	···	2/0.62	···	2/0.21
Crotolaria goreensis	···	···	···	···	···	···	···	···	···	···	···	···	···
Indigofera spicata	···	···	···	···	···	···	···	···	···	···	···	···	···
Lantana camara	7/17.19	1/0.32	···	···	1/0.10	1/0.31	1/0.31	3/0.94	3/0.52	1/0.31	1/0.31	···	1/0.21
Scaevola taccada	6/3.12	8/15.00	2/1.88	1/0.31	8/5.73	7/27.81	4/14.06	···	8/13.96	8/41.25	2/6.25	3/0.94	8/16.14
Stachytarpheta urticaefolia	1/0.31	2/0.62	···	···	2/0.21	1/0.31	···	···	1/0.10	1/0.31	···	···	1/0.10
Ferns													
Nephrolepis biserrata	4/8.75	1/0.31	1/0.31	3/0.94	4/0.42	1/0.31	···	···	1/0.10	3/1.56	1/0.31	···	4/0.62
Ophioglossum petiolatum	···	3/0.94	···	···	3/0.31	···	2/0.62	2/0.62	4/0.42	···	···	···	···
Polypodium scolopendria	7/3.44	6/16.18	2/6.88	6/9.38	8/11.04	8/23.12	6/11.25	5/1.25	8/11.88	8/11.88	4/3.75	6/3.75	8/6.46
Psilotum nudum	4/1.88	1/0.31	···	1/0.31	1/0.21	···	···	···	···	···	···	···	···
Herbs and others													
Alysicarpus vaginalis	3/0.94	···	···	···	···	1/0.31	1/0.31	···	2/0.21	1/0.31	···	···	1/0.10
Calymperes tahitense	7/3.44	2/0.62	1/0.31	6/1.88	7/0.94	1/0.31	1/0.31	4/1.25	4/0.62	···	2/0.62	5/1.25	6/0.73
Cassytha filiformis	5/1.56	···	···	···	···	6/4.38	2/0.62	1/0.31	7/1.77	2/0.62	···	···	2/0.21
Cenchrus echinatus	1/0.31	···	···	···	···	···	···	···	···	···	···	···	···
Chrysopogon aciculatus	4/3.12	···	···	···	···	2/0.62	···	···	2/0.21	···	···	···	···
Cleome rhytidosperma	···	···	···	···	···	···	···	···	···	···	···	···	···
Cynodon dactylon	2/0.62	···	···	···	···	···	···	···	···	···	···	···	···
Cyperus rotundus	···	···	···	···	···	···	···	···	···	4/0.31	···	···	1/0.10
Derris trilobata	1/0.31	···	···	···	···	···	···	···	···	···	···	···	···
Desmodium triflorum	5/1.56	···	···	···	···	···	···	···	···	···	···	···	···
Desmodium sp.	4/1.25	···	···	···	···	···	···	···	···	···	···	···	···
Digitaria ascendens	2/0.62	···	···	···	···	···	···	···	···	···	···	···	···
Emelia sonchifolia	···	···	···	···	···	···	···	···	···	···	···	···	···
Eragrostis tenella	···	···	···	···	···	···	···	···	···	···	···	···	···
Euphorbia cyatophora	3/0.94	···	···	···	···	···	···	···	···	···	···	···	···
Euphorbia geniculata	···	···	···	···	···	···	···	···	···	···	···	···	···
Euphorbia hirta	5/1.56	2/0.62	···	1/0.31	3/0.31	3/0.94	3/0.94	2/0.62	6/0.83	6/1.88	2/0.62	···	7/0.83
Euphorbia prostrata	···	1/0.31	···	1/0.31	2/0.21	···	···	···	···	···	···	···	···
Fimbristylis cymosa	···	4/3.75	1/0.31	1/0.31	5/1.45	···	···	···	···	6/2.50	5/1.56	5/1.56	6/1.88
Hedyotis corymbosa	···	···	···	···	···	···	···	···	···	···	···	···	···
Lepturus repens	1/0.31	1/0.31	1/0.31	2/0.62	3/0.42	···	1/0.31	···	1/0.10	2/0.62	···	···	2/0.21
Luffa cylindrica	···	···	···	···	···	···	···	···	···	···	···	···	···
Mariscus javanicus	3/0.94	4/1.25	···	···	4/0.42	5/1.56	3/0.94	···	7/0.83	6/3.75	2/0.62	···	7/1.46
Passiflora foetida	1/0.31	···	···	···	···	···	···	···	···	···	···	···	···
Phyllanthus amarus	···	4/1.88	3/1.56	4/1.88	4/1.77	···	···	···	···	···	···	···	···
Polygala paniculata	···	···	···	···	···	···	···	···	···	2/0.62	2/0.62	1/0.31	4/0.52
Rhynchelytrum repens	···	1/0.31	···	···	1/0.10	···	1/0.31	···	1/0.10	···	···	···	···
Synedrella nodiflora	···	···	···	···	···	···	···	···	···	···	···	···	···
Tridax procumbens	1/1.25	3/0.94	···	···	3/0.31	4/1.25	5/1.56	1/0.31	6/1.04	2/0.62	3/0.94	···	5/0.52
Vernonia cinerea	2/0.62	1/0.31	1/0.31	4/1.25	5/0.62	3/0.94	1/0.31	1/0.31	5/0.52	6/1.88	2/0.62	1/0.31	7/0.94

* Frequency of occurrence (number of quadrats)/cover percentage (mean for eight quadrats).
† Decade in which mining occurred. Pre-1930 period exceeds a decade; 1980 "decade" includes 1980 through 1982.

APPENDIX

Continued.

1950				1960				1970				1980			
Pit bottom	Scree slope	Rock pinn.	Quadrat avg.	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.	Pit bottom	Scree slope	Rock pinn.	Quadrat avg.
2/2.19	···	···	1/0.73	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	1/0.31	1/0.31	···	2/0.21	···	···	···	···	···	···	···	···
4/1.25	5/2.81	···	8/1.14	1/0.94	2/0.62	···	2/0.52	···	···	···	···	1/0.31	···	···	1/0.10
···	···	2/0.62	2/0.21	···	···	···	···	···	···	···	···	···	···	···	···
···	1/0.94	···	1/0.31	···	···	···	···	···	···	···	···	···	···	···	···
5/2.81	7/5.00	6/4.38	8/3.85	5/4.69	2/3.44	···	6/2.71	···	···	···	···	···	···	1/0.31	1/0.10
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
7/4.69	3/1.56	1/0.94	8/2.40	···	1/0.31	···	1/0.21	···	···	···	···	···	1/0.31	···	1/0.10
···	···	···	···	···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	2/0.62	···	2/0.21	2/0.62	···	···	2/0.21	···	3/0.94	1/0.31	3/0.42	1/0.31	1/0.31	1/0.31	3/0.31
···	···	···	···	···	···	···	···	···	2/0.62	···	2/0.21	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	1/0.31	1/0.10
8/15.00	6/14.38	3/1.56	8/10.31	4/10.00	···	···	4/3.33	1/0.31	···	2/0.62	3/0.31	1/0.31	2/0.62	···	3/0.31
1/0.31	1/0.31	···	2/0.21	···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10
2/0.62	···	1/0.31	3/0.31	8/5.94	5/5.31	5/1.56	8/4.27	5/2.81	7/3.75	6/1.88	8/2.81	1/0.31	8/2.50	7/3.44	8/2.08
3/0.94	2/0.62	···	5/0.52	1/0.31	···	···	1/0.10	···	···	···	···	···	···	···	···
8/10.00	8/3.75	7/2.81	8/5.52	8/5.94	4/1.25	8/6.56	8/4.58	2/0.62	2/0.62	5/1.56	6/0.94	···	2/0.62	4/1.25	6/0.62
···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···	···	···	···	···
···	···	···	···	2/0.62	···	···	2/0.21	1/0.31	2/1.25	···	2/0.52	···	6/1.56	···	6/0.52
6/3.75	4/1.25	8/5.00	8/3.33	···	4/1.25	3/0.94	4/0.73	2/0.62	···	3/0.94	5/0.52	···	···	···	···
2/0.62	···	···	2/0.21	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···
···	···	···	···	···	3/0.94	···	3/0.31	2/0.62	3/0.94	···	4/0.50	2/0.62	8/2.50	···	8/1.04
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
1/0.31	···	1/0.10	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	2/0.62	1/0.61	2/0.31	···	···	···	···
···	···	···	···	···	···	···	···	7/2.18	2/0.62	1/0.31	8/1.04	···	1/0.31	···	1/0.10
···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···	1/0.31	2/0.62	···	1/0.31
···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···
3/0.94	5/1.56	1/0.31	8/0.94	3/0.94	5/1.56	···	8/0.83	···	3/0.94	···	3/0.31	···	5/1.25	···	5/0.42
1/0.31	2/0.62	1/0.31	3/0.42	1/0.31	7/2.19	···	8/0.83	5/1.56	4/1.25	···	5/0.94	2/0.62	3/0.94	···	3/0.52
···	···	···	···	···	···	···	···	1/0.31	···	···	1/0.10	···	···	···	···
···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···
···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10
6/3.75	5/1.56	···	8/1.77	8/8.44	8/5.94	···	8/4.79	4/1.88	2/0.62	···	6/0.83	···	···	···	···
···	···	···	···	1/0.31	1/0.31	···	2/0.21	···	···	···	···	···	1/0.31	···	1/0.10
···	···	···	···	1/0.31	···	···	1/0.10	···	···	···	···	···	···	···	···
···	···	···	···	···	···	···	···	···	···	···	···	···	···	···	···
···	1/0.31	···	1/0.10	···	2/0.62	···	2/0.21	···	1/0.31	···	1/0.10	···	3/0.94	···	3/0.31
···	···	···	···	···	···	···	···	···	1/0.31	···	1/0.10	···	···	···	···
1/0.31	5/2.19	1/0.31	7/0.94	2/1.25	3/1.56	···	5/0.94	1/0.31	5/2.19	···	6/0.83	···	8/3.12	2/0.62	8/1.25
4/1.25	1/0.31	···	4/0.52	1/0.31	7/1.88	···	8/0.73	1/0.31	2/0.62	···	2/0.31	4/1.25	8/3.12	···	8/1.46