J. Plant Res. **108**: 377-386, 1995

Journal of Plant Research

Adaptive Significance of Sprouting of *Euptelea polyandra*, a Deciduous Tree Growing on Steep Slopes with Shallow Soil

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We investigated growth characteristics of *Euptelea polyandra* Sieb. et Zucc. (Eupteleaceae), a Japanese endemic deciduous tree species growing on unstable ground such as that of very steep slopes with thin soil. *Euptelea polyandra* began to sprout at the juvenile stage and had a multiple-stemmed tree form. There was a positive correlation between diameter of the maximum-sized stem within a stool (DMS) and the number of stems within the stool. Many stools had suffered from disturbances as shown by the fact that uprooting scars were found on 31.4% and 42.4%, respectively, of the stools of the two populations studied. Sprouting played a significance role in repairing damaged stems and stools, and at least 15.5% and 18.2% of the stools of the two populations, respectively, had apparently avoided death by sprouting. Sprouted stems gradually inclined with the increase in their relative sizes within each stool, and this seemed to facilitate the establishment of younger sprouted stems. The small younger sprouted stems had their own roots. There were dormant buds on stems which originated from axillary buds, and secondary dormant buds occurred by branching. The total number of dormant buds in a stool increased with DMS. It is concluded that *E. polyandra* accumulates dormant buds for sprouting in order to respond to disturbances quickly.

Key words: Basal dormant bud — Ground-surface disturbance — Repair of tree form — Stool development — Uprooting — Vegetative reproduction

Topographically unstable habitats, where surface materials frequently move, are unfavorable for the establishment and growth of plants. In particular, tree growth is limited on very steep slopes where rapid erosion prevents development of root systems to support the trunks of trees. Sakai and Ohsawa (1994) suggested that the vegetation pattern of a watershed in a hilly region of Japan was largely determined by a regime of ground surface disturbances coinciding with the landforms: around the ridges there was a well-developed evergreen forest, whereas nearly 32% of the watershed was covered by vegetation of poor coverage with a scattering of shrubs and trees. The vegetation was found to be poorly developed in the area of valleys and to be significantly affected by ground surface disturbances such as slope failure and soil erosion. Relatively few species of trees were established at the unstable sites.

However, the tree species *Euptelea polyandra* Sieb. et Zucc. (Eupteleaceae) was observed to be mainly distributed at the unstable sites of the watershed and to dominate there. It is a deciduous sub-tree attaining dimensions of approximately 15 m in height and 30 cm in diameter. It has been found to be distributed in the area of valleys of hills and lower mountains in upper warm-temperate and lower cool-temperate climate regions of Honshu, Shikoku and Kyusyu (Horikawa 1972, Asano 1987). In other areas, it is established on steep slopes with shallow soil (Tohei 1979, Shimada 1994), such as small-scale landslide scars, and on alluvial deposits created by landslides where slope ruptures repeatedly occur (Sakai and Ohsawa 1993).

How does *Euptelea polyandra* grow in unstable habitats? *Euptelea polyandra* frequently sprouts under natural conditions. In general, trees sprout for repair of broken tree architecture (e.g. Hallé *et al.* 1978, Puts and Brokaw 1989). The ability to sprout enables trees to survive disturbances such as fires (Uemura *et al.* 1990, Moravec 1990, Keeley 1992, Shukor 1993) and windstorms (Bellingham *et al.* 1994). Del Tredici (1992) suggested that the high degree of sprouting ability of *Ginkgo biloba* helped to maintain genets where the bases of trees were disturbed by soil movement. Thus, it is suggested that the sprouting ability of *E. polyandra* enables it to grow in unstable habitats where tree architecture may be frequently damaged by ground surface disturbances. In this study, we investigated the growth characteristics of *E. polyandra* in terms of the nature of sprouting, and here in discuss its significance in unstable habitats.

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Materials and Methods

Study area of field examination

Field examinations were conducted on two populations of *E. polyandra* to investigate the stool and sprout structures of the species in the Boso Hills (35°12′N, 140°9′E), Chiba, Japan. The first population is located in a small basin (3.42 ha in projected area) at the head of the Doozawa River, which is a small tributary of the Obitsu River (this is the same basin as that in Sakai and Ohsawa 1994). The second population is located in a small basin (2.39 ha in projected area) at the head of the Kuwanokizawa River, which is 4 km away from the Doozawa River basin. We refer to the two study basins as Plot 1 and Plot 2, respectively. They are in the Tokyo University Forest in Chiba.

Climatical, topographical, geological, and vegetational characteristics of Plot 1 are as follows: altitude, 200 m; annual mean temperature, 14.1C; and annual precipitation, 2,470 mm with a relatively dry winter and humid summer. The basin consists of very steep slopes (40.7 degree on the average) with many small cliffs. The bedrock is soft Tertiary deposits with alternating strata of sandstone and mudstone (Anno-gosou, Iijima and Ikeya 1976). It is highly erodible with large exposed portions in the area of valleys. A warm-temperate forest dominated by evergreen trees such as evergreen *Quercus* spp. and conifers is established at stable sites around the ridge and its branches. On the other hand, *Euptelea polyandra* and some deciduous shrubs dominate the area around the valleys, where repeated ground surface disturbances have occurred (see Sakai and Ohsawa 1994 for details).

The characteristics of Plot 2 are similar to those of Plot 1 except for the age of the forest. The forest has existed for 63 years since the last cutting in Plot 2 and for over 100 years in Plot 1; deciduous trees are more abundant in Plot 2.

Stool and sprout structures

Euptelea polyandra often has a multiple-stemmed tree form (see Fig. 3). We refer to each individual as a stool even if it has only one stem. There are sprouts from the root-collar and the lowest parts of the mother stems (basal sprouts), and from the upper parts of mother stems (trunk sprouts). In Plot 1 and Plot 2, the diameter and inclination of the mother stems, of the basal sprouts, and of the trunk sprouts having their own roots were measured for each stool at 1 m above the ground (D_{100}) if they were long enough to measure. For shorter stems, diameters were measured at 30 cm (D_{30}). The presence or absence of fruit was also recorded for each stem of each stool.

Diameters of dead stems were also recorded, and the ratio of dead stems to all stems in each stool was calculated. It was frequently observed that dead stems and stools had been removed from the standing positions immediately after their death. Thus, the dead stem ratios were calculated except for single-stemmed stools because they are smaller and may be lost rapidly. Dead stems of sprouting stools can be identified by the combination of the scars on the stools and the dead stems coinciding with the scars. The dead stems lying on the ground tend to be downward on the slope from the stools while they decay and finally disappear; therefore, even if all stems of a stool have died, they can be identified quite easily.

Stools in which uprooting scars were found were recorded even if scars were found in only some of the stems within the stools (see the stools in Fig. 3: all had uprooting scars). In most cases, some or many parts of the root systems were still connected to the ground after uprooting. Thus a stool was recorded as the stool which had an uprooting scar if a pit (a hollow due to removal of some root systems) and mound (a complex material of the roots and soil) were observed on the stool concerned, even if the roots were not completely separated from the ground. Slope inclination was measured for each stool in Plot 1 and 2, and soil depth was measured for each stool in Plot 1.

Although the age of a stem can be estimated from its diameter because there is a high positive correlation between them (Sakai and Ohsawa 1993), the age of a stool cannot be estimated because the main stem or main axis of the stem has sometimes changed within the stool. On the other hand, the diameter of the maximum-sized stem in a stool (DMS) is significantly correlated with the total basal area of the stool ($r_s=0.96$; Spearman's test). We hence used DMS as an indicator of stool development in biomass.

Examination of buds

Buds of *E. polyandra* were studied in the laboratory to investigate the origin of sprouts. There were many buds on trunks: some of these buds were isolated from the other buds, whereas others were clustered together (from a few to some scores). Isolated buds near the base of stems, (basal buds) were sampled from three stems with diameters of 1.3, 6.4 and 23.6 cm to examine the buds morphologically in Plot 1 in late November. Samples were fixed with FAA (formalin, acetic acid, and 50% ethanol, 1:1:18). Bud scales were removed from some of the samples for scanning electron microscopy. The samples were dried by a critical point dryer, HCP-2, coated with gold at 1.2 kv for 15 min. in an ion-sputter, JFC 1100, and examined using a scanning electron microscope, JSM-25S, at an acceleration voltage of 15 kv.

To estimate sprouting ability of the stems of *E. polyandra*, numbers of buds were counted for all of the 167 living stems longer than 50 cm except for current year parts for 61 stools selected randomly in Plot 1. We counted only the buds which were on the lowest part of main stem (between the root-collar and 50 cm above the root-collar).

Results

Structure of basal sprouts

There were 49.7 stools and 132.9 stems (>1 m in length) per hectare in Plot 1 and 27.7 stools and 130.4 stems (>1 m in length) per hectare in Plot 2. The maximum diameters were 25.3 cm and 33 cm in Plot 1 and Plot 2, respectively. Figure 1 shows the frequency distributions of diameters in Plot 1 and Plot 2. The diameter distributions of all stems were biased to smaller sizes, whereas, the distributions of stools, which were represented by the distributions of the diameters of the maximum-sized stems in the stools (DMS), were relatively flat.

Euptelea polyandra began to sprout at the juvenile stage. Figure 2 shows the ratios of stools having more than one stem (sprouting stools) and the stools having fruiting stems (fruiting stools) in relation to DMS. The number of sprouting stools increased as DMS became large, and almost all of the stools had sprouts when DMS reached 10 cm. The fruiting stools also increased with DMS, but the numbers of fruiting stools were always smaller than the numbers of sprouting stools until almost all of the stools had fruiting stems (>20 cm). The distributions of the DMS of the sprouting stools were significantly biased to smaller classes than the distributions of the DMS of the fruiting stools in Plot 1 ($p=0.009$; Kolmogorov-Smirnov test), but there was no significant difference between them in Plot 2.

Euptelea polyandra sprouted continuously during its development. The number of stems within a stool increased with DMS ($p=1.5$ E-29 in Plot 1 and $p=1.4$ E-10 in Plot 2; Spearman's tests). As a result *E. polyandra* often had a well-developed multiple-stemmed tree form consisting of stems of various sizes (Fig. 3a). The typical mature (fruiting) stool had one to three major stems forming its crown, and many smaller stems (<2 cm in diameter) around the root-collar and on the lowest parts of the major stems.

Basal sprout stems began to have their own roots (Fig. 3d) at the small stage, at least 50 cm in height. Trunk sprouts near the ground also had roots (Fig. 3f).

Habitat condition and damage to stools

The slope inclination and soil depth at the sites where *E. polyandra* was located were 46.8 degrees and 13.6 cm on the average in Plot 1, significantly steeper ($p=0.0011$ with a t-test) and thinner ($p=3.0$ E-9; Kolmogorov-Smirnov test) than the values for the whole area of the plot 1 basin reported by Sakai and Ohsawa (1994). It was confirmed that *E. polyandra* was situated at considerably erodible sites within the area. Slope inclinations averaged 50.2 degrees at the sites where *E. polyandra* was found in Plot 2.

A large part of the stools had been uprooted (Fig. 4), probably due to the steep slope and thin-soil conditions. Uprooting scars were found on 61 of the 194 stools (31.4%)

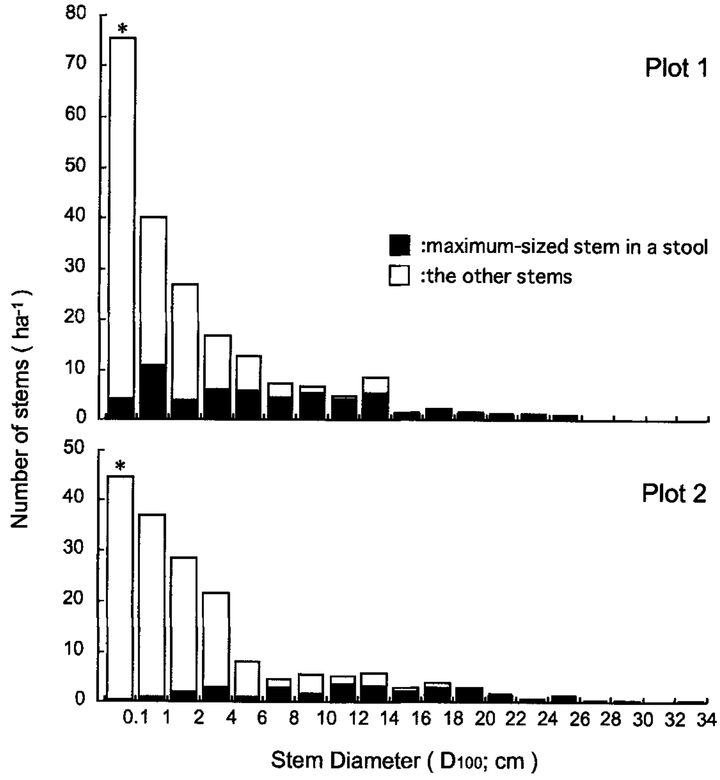


Fig. 1. Frequency distribution of stem diameters at 1 m above ground of *Euptelea polyandra* at each study site. Solid bars represent the number of maximum-sized stems in a stool in each size class. Asterisks in the figure indicate the number of stems whose diameters were measured at 30 cm above the ground.

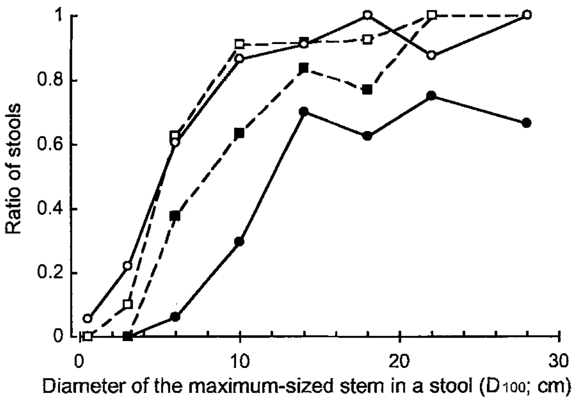


Fig. 2. Ratios of stools having multiple stems in Plot 1 (open circles) and in Plot 2 (open squares), and stools having fruiting stem(s) in Plot 1 (closed circles) and in Plot 2 (closed squares).

in Plot 1 and on 28 of the 66 stools (42.4%) in Plot 2. There was no correlation between the ratio of stools having uprooting scars and diameter size class ($r_s=0.43$ in Plot 1 and $r_s=0.05$ in Plot 2; Spearman's tests).

Dead stems of multiple-stemmed stools constituted 140 of 619 stems (22.6%) in Plot 1 and 169 of 400 stems (42.0%) in Plot 2 (Fig. 5). There was no correlation between the ratio of dead stems and diameter size class ($r_s=-0.17$ in Plot 1 and $r_s=-0.59$ in Plot 2; Spearman's tests). In spite of the high mortality of stems, there were only two stools (2.1% of the total) in Plot 1 and one stool (2.0% of the total) in Plot 2 in which all stems among the multiple-stemmed stools had died. There were 18 of 194 stools (9.3%) in Plot 1 and 5 of 66 stools (7.6%) in plot 2 whose maximum-sized stem had died but in which other stem(s) were living.

Stem inclination and stool development

Figure 6 shows the relationship between diameter and inclination of living stems which belonged to single-stemmed stools (Fig. 6b) and multiple-stemmed stools (Fig. 6a). In both single and multiple-stemmed stools, larger stems had high inclinations; the averages of the inclinations of mature stems (fruiting stems: >ca. 10 cm in diameter) were 46.5 degrees in Plot 1 and 56.8 degrees in Plot 2, and there was no significant difference between the mature stems belonging to the single and multiple-stemmed stools. The smaller stems of single-stemmed stools (≅seedling stems) also inclined as much as the mature stems; there was no significant correlation between diameter and stem inclination. The smaller stems of the multiple-stemmed stools (sprout stems), however, showed a tendency to stand upright; there was a positive correlation between diameter and stem inclination ($p=1.2\,E\text{-}25$ in Plot 1 and $p=4.4\,E\text{-}22$ in Plot 2; Spearman's tests).

Figure 7 shows the relationship between the order of diameter in a stool, numbered from the smallest to the largest within single stools, and the order of stem inclination in a stool, numbered from the one with the least inclination to the one with the greatest inclination. It was clear that stems gradually inclined with the increase in their relative sizes within each stool.

Morphology of dormant buds

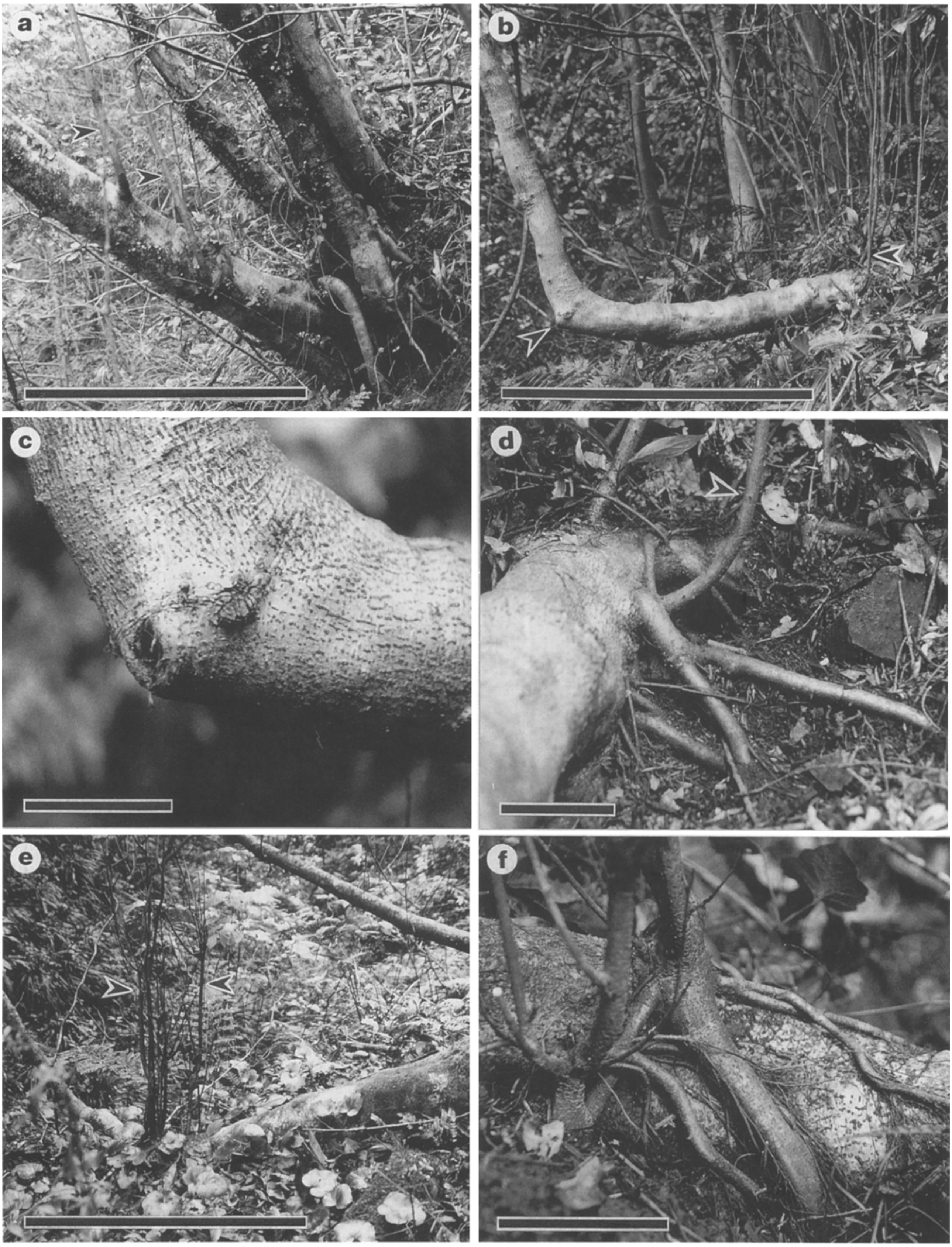
Euptelea polyandra had many basal buds on stems (Figs. 8b and 8e). The isolated type buds increased in size with diameter of stem (Fig. 8a). They were anatomically different from the normal winter buds (Figs. 8g and 8h). As shown in Fig. 8c, the basal buds; had many small bud scales (e.g., 53 scales were counted on a 6.4 cm stem in another sample), while the winter buds normally had seven to nine scales. There were no preformed leaves inside the basal buds (Fig. 8d), while there were such leaves inside the winter buds (Fig. 8h). We observed that basal bud traces connected to the pith of stems in young stems, and that the basal buds were arranged in a manner similar to the leaf arrangement. These findings indicated that the basal buds of the isolated type of *E. polyandra* were dormant buds originating from axillary buds and that they remained on the bark (Aaron 1946, Kozloski 1971, Kauppi *et al.* 1987).

Some or many basal buds were sometimes found be clustered together on bark (clustering buds; Fig. 8e). The traces of these buds were connected in the wood (Fig. 8f). This indicates that they occur secondarily; they might originate in the axils of the scales of a dormant bud (Kauppi *et al.* 1987), or they might be winter buds on a short shoot which have become dormant (Kozlowski 1971).

Number of dormant buds

There was no significant correlation between diameter and bud number ($p=0.61$; Spearman's test, Fig. 9). However, variances of the total bud numbers were significantly different among diameter classes, 0.1-1 cm (D_{30}), 0.1-2 cm (D_{100}), 2-24 cm (D_{100}), and the variances were larger in this order ($p<0.0007$; *F*-tests using the logarith-

Fig. 3. Tree forms of *Euptelea polyandra*. a) A well-developed stool of *E. polyandra* consisting of some basal sprout stems. Arrows in the figure indicate trunk sprouts from a inclined stem. The bar shows 1 m. b) A stool having an elbow-shaped bent stem. The arrow on the left indicates the picture position of (c) and the one of the right indicates a young basal sprout. There are also many other young basal sprouts around the indicated sprout. The bar shows 1 m. c) There is a scar of the old main axis of the stem at the bending point of the elbow-shaped stem indicated in (b). The bar shows 10 cm. d) A young basal sprout (arrow) and its root system connected with the mother stem. This sprout stem is the same as the one indicated in (b). The bar shows 10 cm. e) Trunk sprouts (arrows) from a uprooted lying stem. The bar shows 1 m. f) The lower part of the trunk sprouts indicated in (e). The sprout stems develop root systems which grow across the mother stem and become established in the ground. The bar shows 10 cm.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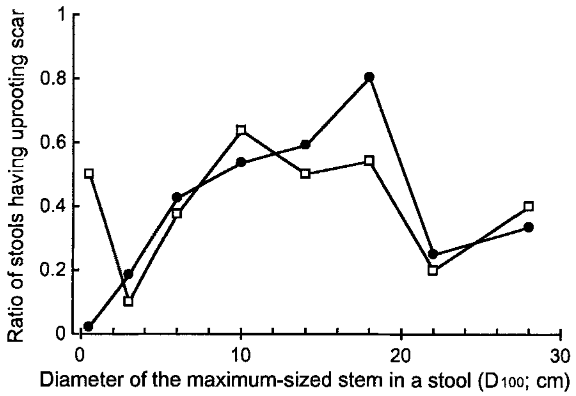

Fig. 4. Ratios of stools having uprooting scars which indicate that the stools have been fully or partially uprooted. Closed circles and open squares show the ratios in Plot 1 and in Plot 2, respectively.

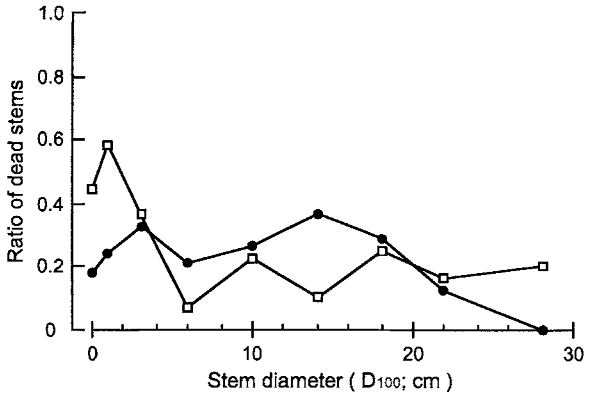

Fig. 5. Number of dead stems per all stems of multiple-stemmed stools in Plot 1 (closed circles) and in Plot 2 (open squares).

mic transformed value of bud number). This was because large stems sometimes had many clustering-type buds (Fig. 8e), although the number of isolated type buds gradually decreased ($p=0.000007$; Spearman's test) as the diameter increased. The number of clustering type buds tended to increase with the stem size ($p=0.00018$; Spearman's test).

There was a high positive correlation ($p=3.28$ E-14; Spearman's test) between the DMS and the total bud number of a stool (Fig. 10), although there was no correlation for each stem as mentioned above.

Discussion

Our results allow us to draw a schematic diagram of the stool development of *E. polyandra* (Fig. 11). Scale of age in the figure indicates estimated ages of the maximum-sized stem in a stool based on the age-diameter relationship obtained on a slope in a basin neighboring Plot 1 (Sakai and Ohsawa 1993). *Euptelea polyandra* is established as a single stem, and immediately starts to produce

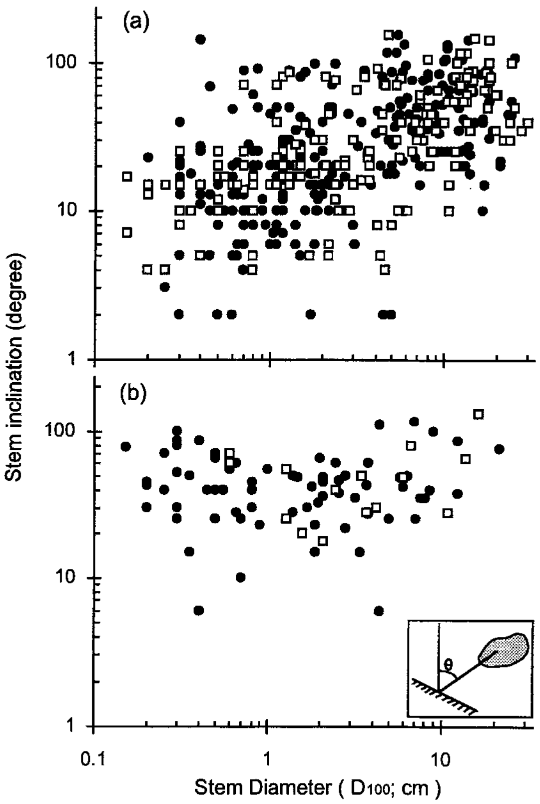

Fig. 6. Inclinations of living stems belonging to (a) multiple-stemmed stools and (b) single-stemmed stools. Closed circles and open squares show the stems in Plot 1 and in Plot 2, respectively.

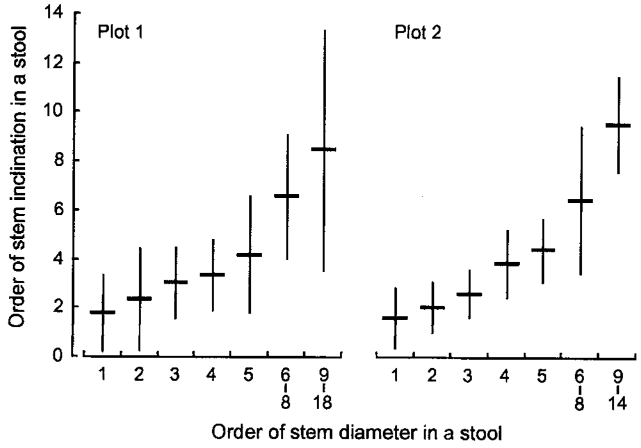

Fig. 7. Relationship between relative size and relative degree of inclination of stems within a stool. For the living stems measured at 1 m above the ground, they are numbered in the order of diameter from the smallest to the largest and in the order of degree of inclination from the one with the least inclination to the one with the greatest inclination in each stool having multiple stems. Averages with standard deviations (vertical bars) are shown.

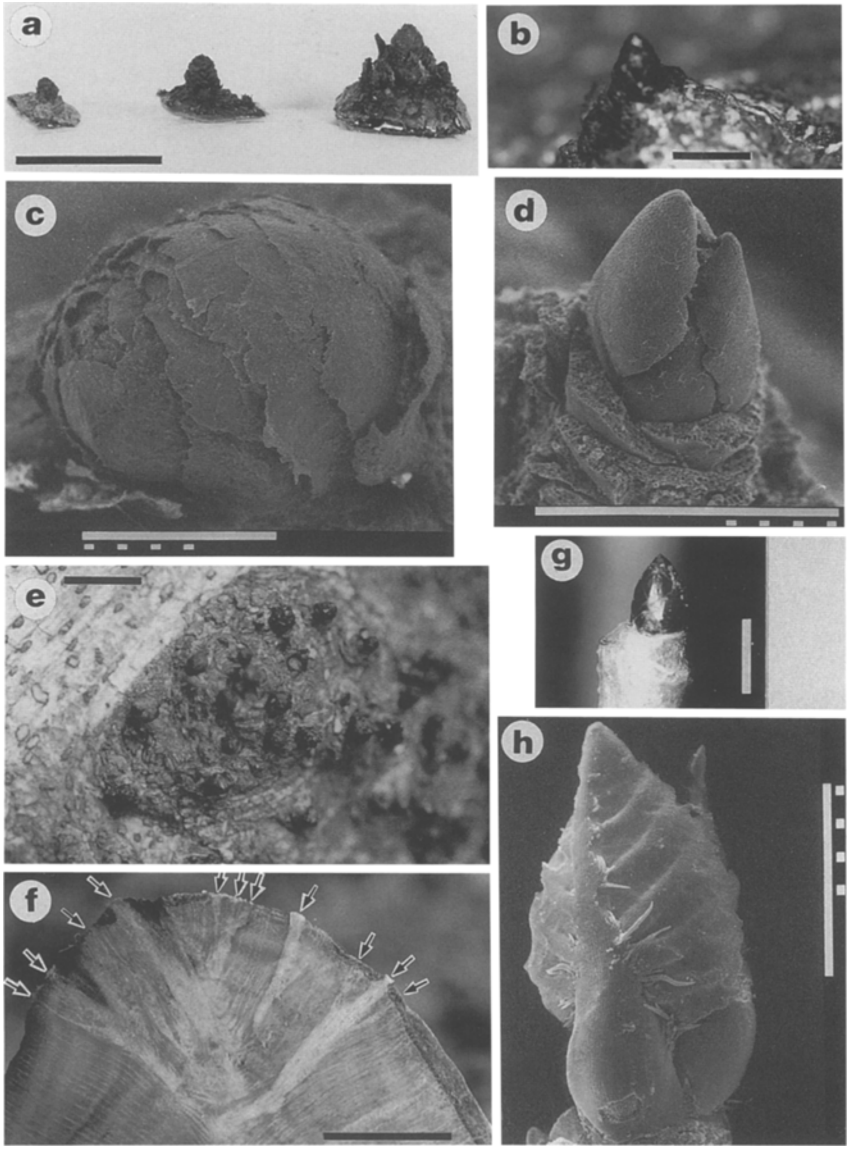

Fig. 8. Buds of *Euptelea polyandra*. a) Samples of isolated-type buds (see text) fixed with FAA which were on the lower parts of stems. The buds on the left, on the middle and on the right were on stems having diameters (D_{100}) of 1.3, 6.4, and 23.6 cm, respectively. The bar shows 1 cm. b) An isolated-type bud on a stem. The bar shows 5 mm. c) A scanning electron micrograph of an isolated-type basal bud obtained from a stem with a diameter (D_{100}) of 1.3 cm. The bar shows 1 mm. d) A scanning electron micrograph of an isolated-type basal bud from a stem with a diameter of 6.4 cm. Bud scales were removed. There are preformed fresh bud scales inside of the removed bud scales. The bar shows 1 mm. e) A cluster of buds on the lower part of a stem with a diameter (D_{100}) of 18.8 cm. The bar shows 1 cm. f) A crosscut of wood under a cluster of buds. Arrows indicate the position of buds, which were broken for handling. The bar shows 1 cm. g) A typical winter bud of *E. polyandra*. The bar shows 5 mm. h) A scanning electron micrograph of preformed leaves in a winter bud. The bar shows 1 mm.

dormant buds for sprouting. *Euptelea polyandra* initiates sprouting at the juvenile stage ; it allocates resources to sprouting before it commences reproduction by seeds. Almost all *E. polyandra* trees have sprouted when the maximum-sized stem in a stool has attained an age of about 25 years (10 cm in diameter), while about only half of them have started seed production. The sprouted stems initially stand upright and gradually incline. Thus, a well-developed *E. polyandra* tree has a multiple-stemmed tree form in which stems are arranged in a manner such that much older stems are much more greatly inclined.

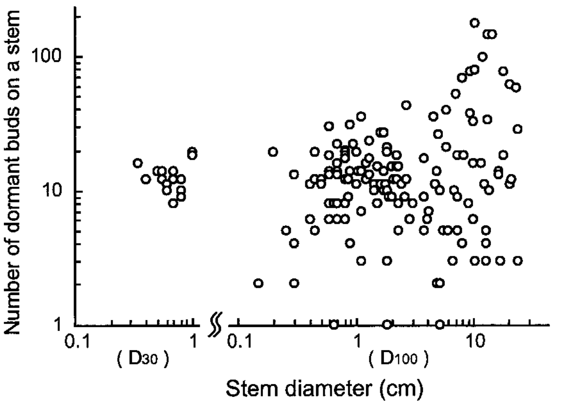

Fig. 9. Numebr of dormant buds on lower part of stem between the root-collar and a point 50 cm above the root-collar.

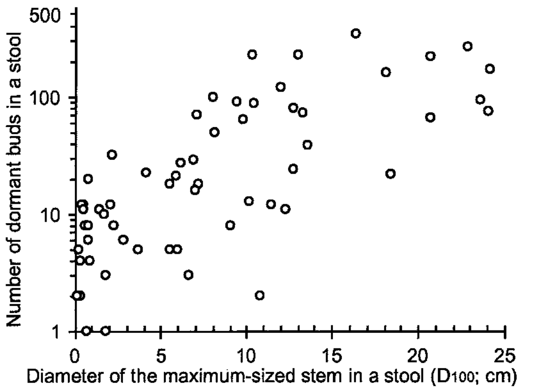

Fig. 10. Total number of dormant buds on stems (see Fig. 10) within a stool.

A function of sprouting is to repair damaged stems and stools. This is very important for *E. polyandra* because it grows under conditions where disturbances frequently occur. Stems cannot stand upright due to the steep inclination and the thin soil unless roots of the mother stem support them, and 30-40% of the stools experience uprooting. Although causes of stem death were not identified in this study, it is thought that the main cause of death of large-sized stems was ground-surface disturbance, because it was frequently observed that dead stems, particularly large-sized dead stems, were completely uprooted or snapped, probably due to great inclination. There are two lines of evidence indicating that *E. polyandra* can avoid the death of the whole stool by sprouting. The first is the alternation of main stems; even though the maximum-sized stem of the stool concerned had died, younger stem(s) were alive in 18 stools (9.3%) in Plot 1 and five (7.6%) stools in Plot 2. The second is the repair of the form of the main stems; the maximum-sized stems of 12 stools (6.2%) in Plot 1 and seven stools (10.6%) in Plot 2 had elbow-shaped bent stems as shown in Fig. 3b. Each bent stem had a dead stem scar at the bending point (Fig. 3c). This indicates that trunk sprouts on inclining or uprooted stems (Figs. 3a and 3e) had taken the place of the main axes of the stems. As a result, at least 30 stools (15.5%) in Plot 1 and 12 stools (18.2%) in Plot 2 can be considered to have avoided death of the whole stool by sprouting.

Euptelea polyandra maintains dormant buds on the stems. The total number of dormant buds within a stool increases with the development of the stool. This is because each of the sprouted stems has its own dormant buds, and because in larger stems there are sometimes many dormant buds which proliferate secondarily. A

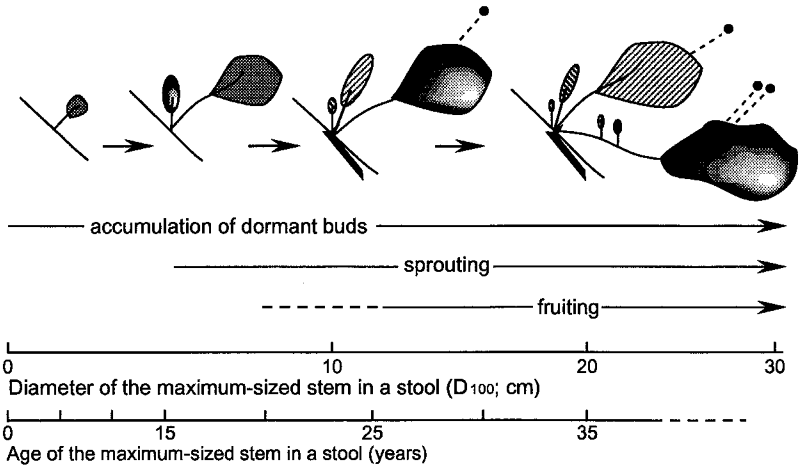

Fig. 11. A schematic of the stool development of *Euptelea polyandra*. Scale of age in the figure is drawn based on age-diameter relationship obtained on a slope in a basin neighboring Plot 1 (Sakai and Ohsawa 1993). The crowns of the same stems are filled with the same patterns. In the right two stools, horizontal black bars and black dots with dotted lines express dead stems and dispersed seeds, respectively.

similar accumulation of dormant buds is also kuown in some tree species such as *Betula pubescence* (Kauppi *et al.* 1987, 1988) and *Quercus dentata* (Hasegawa 1984), which sprout under natural conditions. Harper (1977) referred to accumulated dormant buds as a bud bank, an analogy to a seed or a seedling bank. The bud bank may be an insurance against mechanical damage. In this study, no relationships were found between diameter size and the ratio of uprooted stools, nor between diameter size and the ratio of dead stems. Thus, *E. polyandra* suffers constantly high rates of damage and high risk of death throughout its life history. *Euptelea polyandra* may reserve bud banks in order to respond quickly to these constantly high rates of disturbances.

Irrespective of the high ratio of uprooted stools, there were surprisingly fewer stools which died completely. That is, uprooting of *E. polyandra* does not necessarily mean its complete death. This may be partially due to the type of uprooting. *Euptelea polyandra* has no apparent main root and has many thin roots elongating horizontally (Karizumi 1979). Roots run on the bedrock underlying shallow soil and grow into cracks in the bedrock. Thus, after a stem is uprooted, roots are still connected with the soil at the downward side of the tree. Moreover, the roots are often connected or bridged to the upward side of the pit. This is similar to the 'hinge-tear' type of uprooting reported by Cook (1971) and Schaetzl *et al.* (1989) in Wisconsin. According to them, the hinge-tear type is common on Histosols where soil shear strength is low. Koop (1987) also recognized that there is a type of uprooting in which some roots remain connected to the soil after uprooting in some European deciduous forests. He noted that such uprooting doesn't mean immediate death of the individuals.

Sprouting of *E. polyandra* may also have a function of vegetative regeneration. *Euptelea polyandra* seems to sprout inherently without distinct disturbances because almost all individuals have sprouts except for very young stems. Moreover, the small sprouted stems already have their own root systems (Figs. 3d and 3f). Therefore, the purpose of the sprouting of *E. polyandra*, also, may be not only for repair of damaged stems or stools but also for the establishment of new stems. Vegetative regeneration by sprouts is thought to be used for compensation of the low opportunity for the establishment of seedlings (e.g., Johnston and Lacey 1983, Ohkubo 1992, Bellingham *et al.* 1994). For example, Ohkubo (1992) reported that basal sprouting of *Fagus japonica* had such a function in a Japanese cool-temperate forest where dense dwarf bamboo prevented seedling establishment. *Euptelea polyandra* is also thought to have a low opportunity for seedling establishment, because there were considerably fewer stools whose DMS's were small ($\cong$seedling stems) in the basins in contrast to many stems having seeds (ca. $\geq$10 cm in diameter). Moreover, even if seedlings are successfully established, they cannot grow upright due to unstable ground. On the other hand, sprouted stems are on mother stems at least during youth and can grow upright. Although sprouted stems also gradually incline coinciding with their growth, the inclination of older stems seems to facilitate the establishment of younger sprouting stems, i.e., inclination of the foliage of the older stems allows the younger sprouting stems to have more sunlight. As a result, re-establishment with sprouts would appear to be more advantageous than re-establishment with seeds. This may be one of the reasons why *E. polyandra* allocates resources to sprouting before it starts reproduction by seeds.

In some European deciduous forests, Koop (1987) argued that vegetative reproduction of trees (including sprouting) seems to be particularly important under circumstances where natural growth is difficult, e.g., near the limits of tree growth. Our study proposes that sites on steep slopes with thin soil are also habitats where sprouting ability becomes useful.

We wish to thank Dr. S. Sakai for his critical comments on the manuscript. We would also like to thank the members of the staff of the Tokyo University Forest in Chiba for their generous help and cooperation for doing field survey in their experimental forest. We are pleased to acknowledge the considerable assistance of Dr. Kitahara and the other members of National Grassland Research Institute. We also wish to thank Dr. T. Ohkubo for helpful advice.

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(*Received February 20, 1995: Accepted July 18, 1995*)