IMPACTS OF PASTORALISTS ON WOODLANDS IN SOUTH TURKANA, KENYA: LIVESTOCK-MEDIATED TREE RECRUITMENT[1]

ROBIN S. REID[2] AND JAMES E. ELLIS[3]
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80526 USA

Abstract. Since the turn of the century, African pastoralists have been held responsible for overuse of woody plants and for the degradation and desertification of many arid and semiarid lands. We analyzed the impacts of pastoral nomads and their livestock on the recruitment (establishment to first reproduction) of *Acacia tortilis,* a dominant tree in the dry woodlands of South Turkana, Kenya, where *Acacia* seedpods make up an important part of livestock diets. Seed density averaged over 85 times higher in bush-fenced livestock corrals than in the surrounding environment. The survival and growth of 14 cohorts of trees ranging in age from 1 to 39 yr were investigated comparing tree stands originating inside livestock corrals with those originating outside. Corral soils contained nine times more C, three times more N, and six times more P than adjacent noncorral soils immediately following corral abandonment. Corral soils also retained more moisture than noncorral soils after rainfall. These soil conditions accelerated seedling emergence in corrals, and enhanced survival and growth of 1st-yr seedlings. Survival of older trees in corral stands was not significantly different from those established outside corrals during this study. However, comparison of tree densities over time suggests that corral stands thin more rapidly than noncorral stands, probably because of crowding. The early survival and growth advantages of the corral environment appear to stabilize the reproductive patterns of *A. tortilis* in this arid ecosystem, where successful recruitment in noncorral sites may be restricted to the few years with high rainfall. Contrary to the conventional wisdom, pastoralists may be improving rangelands in South Turkana by enhancing recruitment reliability in this important tree species.

Key words: Acacia tortilis; arid ecosystem dynamics; dry tropical woodlands; Kenya; livestock; pastoralists; population ecology; seed dispersal; seedling emergence; seedling establishment; seedling survival; tree recruitment.

INTRODUCTION

For over half a century, African pastoralists and their livestock have been blamed for overuse of woody plants and desertification throughout arid and semiarid zones (Stebbings 1935, Charney et al. 1975, Lamprey 1983, Sinclair and Fryxell 1985). Loss of vegetative cover and lack of tree regeneration caused by heavy browsing, grazing, and woodcutting are said to initiate a sequence of processes that feed back on local climate, causing a sustained decrease in rainfall (Charney et al. 1975, Schlesinger et al. 1990). Even though the existence of widespread desertification in Africa is now questionable (Binns 1990, Hellden 1991, Tucker et al. 1991, Dodd 1994), the assumption of pervasive negative human impacts on woodlands continues to shape policy and management guidelines for arid lands (Forse 1989, UNEP 1991, Ellis 1994).

Trees play a central role in the structure and function of arid land ecosystems and in the exploitation strat-

egies of pastoralists who occupy those ecosystems. The deep roots of trees provide access to soil water during dry seasons and droughts. Thus tree foliage remains green longer than herbaceous plants, providing high quality browse to herbivores and much-needed shade for animals and people during the heat of the day (Le Houérou 1980, Coughenour et al. 1985, Galvin 1985). Furthermore, tree seedpods supply protein, phosphorus, and carotene to animal diets during dry seasons when the quality of herbaceous forage drops dramatically (Pratt and Gwynne 1977, Coppock et al. 1987, Le Houérou 1989). Tree shade slows the desiccation of understory herbs during dry periods (Bernard-Reversat 1982, Tolsma et al. 1987), and tree understory soils are routinely higher in fertility and moisture (Maranga 1986, Belsky et al. 1989) and often support entirely different complements of herbs that are both more productive and nutrient-dense than those in sunlit gaps (Tolsma et al. 1987, Belsky et al. 1989, Weltzin and Coughenour 1990). Because many trees are highly drought resistant, tree-dominated ecosystems may resist forces that drive system-level shifts in vegetation physiognomy (e.g., Archer 1989) or transitions in ecosystem state (Westoby et al. 1989); tree planting is commonly prescribed to reverse desertification (Steppler and Nair 1987).

[2] Present address: International Livestock Research Institute (ILRI), P.O. Box 30709, Nairobi, Kenya.
[3] Present address: Centre for African Ecology, University of Witwatersrand, Johannesburg, South Africa.

FIG. 1. Photograph of a livestock corral supporting trees ≈13 yr in age, where a family of pastoralists kept goats in February 1975.

This investigation was part of a long-term study, the South Turkana Ecosystem Project which, among other objectives, sought to clarify the role of nomadic pastoralists in the dynamics of dry woodlands. Previously, it was determined that Ngisonyoka pastoralists in South Turkana each year harvest 5% or less of the current annual growth of tree biomass for fuelwood, housing, fencing, tools, and utensils (Ellis et al. 1984, Coughenour et al. 1985). Other studies noted that the Ngisonyoka feed the abundant, high-protein seedpods of the dominant tree, Acacia tortilis (Forsk.) Hayne subsp. spirocarpa (Hochst. ex A. Rich.), to young and milking livestock (Coppock et al. 1986) during periods when other forage sources were of much lower quality. Many of these seeds pass through the livestock digestive system intact and are deposited in corrals where sheep/goats or camels spend the night. We observed that during the first rainy season after pastoralists abandon their corrals, Acacia seeds germinate, creating dense circular patches of seedlings in old corrals (Fig. 1; J. E. Ellis et al., unpublished data). Because the Ngisonyoka move very frequently (13 times per year on average, McCabe 1985), the landscape is replete with abandoned homesites (awis) and Acacia stands, which originated in livestock corrals.

Objectives

The overall objective of this study was to determine the influence of corralling on recruitment (defined here as seed redistribution and germination, seedling emergence, and survival to reproductive maturity) of the flat-top thorn tree, A. tortilis. We compared soil characteristics and tree population patterns and processes between adjacent corral and noncorral sites. However, field observations suggested that both landscape position (riparian vs. upland) and tree cover (under tree canopies vs. in gaps between canopies) might also be important to the recruitment of this species. Therefore, even though the primary focus was on corral environments, we explicitly included landscape position and tree cover in the design. We then asked five questions about the interaction between corrals and tree population dynamics: (1) How do livestock affect the distribution of seeds on the landscape? (2) How do corral and noncorral soil environments differ? (3) How does emergence, growth, and survival of trees differ between corral and noncorral sites? (4) Do the effects of corral environments on population processes vary from year to year? (5) What do these results imply for the role of pastoralism in the recruitment of A. tortilis in Turkana?

The study area

The Ngisonyoka Turkana are nomadic pastoralists, still engaged in a relatively traditional lifestyle at the time of this study in 1987–1988. They subsist mostly on milk, meat, and blood from their herds of cattle, camels, sheep, goats, and donkeys, and they move continuously in response to temporal changes in livestock forage availability (Coughenour et al. 1985, Galvin 1985, McCabe 1985). Their 9000-km² territory is in the southern part of Turkana District in northwestern Kenya, to the south and west of Lake Turkana within the Gregory Rift Valley. Annual rainfall in this area varies from ≈600 mm per annum at the southwestern boundary of Turkana District to <200 mm at the other edge of Ngisonyoka territory, 90 km to the north. About 60% of the precipitation falls in April and May, with occasional rain events in October or November (Little and Johnson 1984). Drought years occur on average every 4–5 yr, sometimes resulting in almost complete failure of primary production; sequential drought years

cause substantial losses of livestock. Frequent droughts also prevent the components of the ecosystem from converging on a self-regulated biological equilibrium, thus the population patterns of plants, animals, and people are unstable and highly periodic or dynamically nonequilibrial (Ellis et al. 1987, 1991, Ellis and Swift 1988, Leslie and Fry 1989).

The landscape of Ngisonyoka territory is dominated by a low range of basement-complex mountains (2000-m peaks), which run north–south, parallel to the Rift Valley wall. The mountains are surrounded by moderately sloping pediments that flatten onto alluvial bajadas (600 m), variegated by intermittent stream beds. The streams flow into the Turkwell River on the west and into the Kalapata River, at the foot of a Miocene basaltic plateau, on the east. The alluvial soils are deep, poorly differentiated sands or sandy loams (Patten 1991) with rapid infiltration rates; soils have low water-holding capacities, organic matter, soil nutrients, and cation exchange capacity (Coppinger 1987). The alluvial plains, pediments, and mountains support annual grasses and forbs (*Aristida, Eragrostis, Gisekia* spp.), dwarf shrubs (*Indigofera, Sericocomopsis* spp.), bush and trees (*Acacia, Commiphora, Salvadora, Boscia* spp.) (Coughenour et al. 1990*a*). Woody canopy cover varies from 2–100%, usually 10–40% (Coughenour and Ellis 1993), and most large trees are clustered along the intermittent stream beds where underground water remains accessible during much of the long dry season. These riparian woodlands are dominated by *A. tortilis,* the subject of this study (Fig. 2, Wyant and Ellis 1990).

The nomadic cycle of the Ngisonyoka varies annually, but most often it involves a circumnavigation of the basement-complex mountain range. The bajadas and plains surrounding the mountains are dotted with abandoned homesites; circular corral stands of *A. tortilis* are most prevalent along the dry eastern flank of the mountains where the Ngisonyoka traditionally spend the wet season and as much of the dry season as the forage supply will allow. Here, annual rainfall ranges from around 200 mm in the north to almost 400 mm at the other end of the bajada, 40 km to the south (Coughenour et al. 1990*b*). This area was the primary study site for this research.

METHODS

The study design was divided into three parts: measurement of soil nutrients and moisture, the seed and seedling study of the 1987 and 1988 cohorts, and the study of older tree cohorts. The soil nutrient study was completed in 1983 by Ellis et al. (J. E. Ellis, D. Schimel, M. Coughenour, T. Hart, J. Wyant, and S. Lewis, *unpublished data*), and soil moisture was measured in 1988 as part of this study. Both these and the older cohort study were designed as paired comparisons of corral and noncorral sites. The most complicated design, involving a hierarchical nesting of stream beds,

FIG. 2. Photograph of the distinctive pattern of interleaved riparian zones with dense tree cover and more sparsely-treed uplands.

sites, and subsites, applied only to the seed and seedling study.

Soil nutrients and moisture

Ellis et al. (*unpublished data*) sought to quantify effects of corrals on soil nutrients and the changes in soil nutrient content over time; their data are presented here. They analyzed soil samples from 10 corrals with trees ranging in age from 6 mo to ≈20 yr, and from adjacent noncorral sites. Since corral age was estimated from tree ring counts and older trees appear to skip a ring ≈1 out of every 5 yr due to drought (Wyant and Reid 1992), trees in this analysis are probably slightly older than ring counts indicate.

They performed standard nutrient analyses on the soil samples for C, N, and available P (NaHCO$_3$ extractable), at the Kenya National Agricultural Laboratories, Nairobi.

During the present study, gravimetric soil moisture was measured to quantify soil moisture differences caused by corral environments. Soils were collected and the depths of wetting fronts were measured during the 1988 rainy season at random locations (using randomization methods of Skalski 1987) in five recently abandoned corrals and five adjacent noncorral sites. Soil moisture was measured at four soil depths, selected to characterize soil moisture in the dung layer (corrals
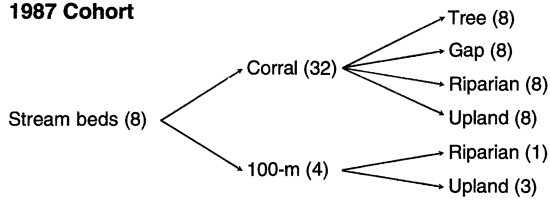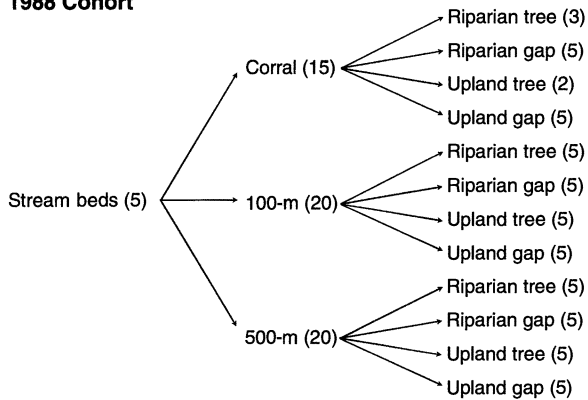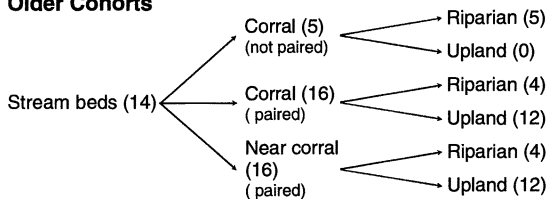
1987 Cohort

Stream beds (8)
- Corral (32)
  - Tree (8)
  - Gap (8)
  - Riparian (8)
  - Upland (8)
- 100-m (4)
  - Riparian (1)
  - Upland (3)

1988 Cohort

Stream beds (5)
- Corral (15)
  - Riparian tree (3)
  - Riparian gap (5)
  - Upland tree (2)
  - Upland gap (5)
- 100-m (20)
  - Riparian tree (5)
  - Riparian gap (5)
  - Upland tree (5)
  - Upland gap (5)
- 500-m (20)
  - Riparian tree (5)
  - Riparian gap (5)
  - Upland tree (5)
  - Upland gap (5)

Older Cohorts

Stream beds (14)
- Corral (5) (not paired)
  - Riparian (5)
  - Upland (0)
- Corral (16) (paired)
  - Riparian (4)
  - Upland (12)
- Near corral (16) (paired)
  - Riparian (4)
  - Upland (12)

FIG. 3. Design and sample sizes for seed and seedling study showing hierarchical nesting of stream beds, sites, and subsites.

only), at the surface (1–5 cm), among grass roots (15–20 cm), and below grass roots (50 cm, maximal grass root depth = 27.7 ± 7.8 cm, mean ± 1 SD, $n = 6$). Soil samples were collected 24 h and 15 d after hard rain; 15 d was the maximum period without rain during sampling. Rainfall was not measured at these sites.

A drying experiment was conducted under controlled conditions to measure soil drying rates. Twenty-four polyvinyl chloride tubes (open-ended, 75 cm long, 10.2 cm diameter) were buried in a grid pattern in sandy loam soil. Each tube was filled with sandy loam and wetted to field capacity. Half the tubes were covered with 5 cm of goat/sheep dung to simulate corral conditions. Each tube was randomly assigned a drying period of either 1, 5, 10, or 25 d. At the end of each period, soils were collected at 1–5, 15–20, and 50 cm. For both this experiment and soil moisture measurements, soils were first weighed to obtain wet mass, dried for 24 h in a black box in the sun, and then reweighed for calculations of percent water content by mass. Preliminary trials showed that soils lost no further mass after a 24-h drying period.

Site selection and study design—seed and seedling study

The design of the seed and seedling study involved a three-level hierarchical nesting of stream beds, sites, and subsites, so that the effects of corral environments, landscape position, and tree cover could be distinguished (Fig. 3). Stream beds ($n = 8$ in 1987, $n = 5$ in 1988) were selected randomly from those that supported many abandoned homesites in the primary study site (stream bed scale, Fig. 4). Turkana homesites and corrals tend to be clustered along the outer edge of the narrow riparian woodlands, which border these intermittent stream beds, although homesites also occur on the intervening uplands and within riparian woodlands as well.

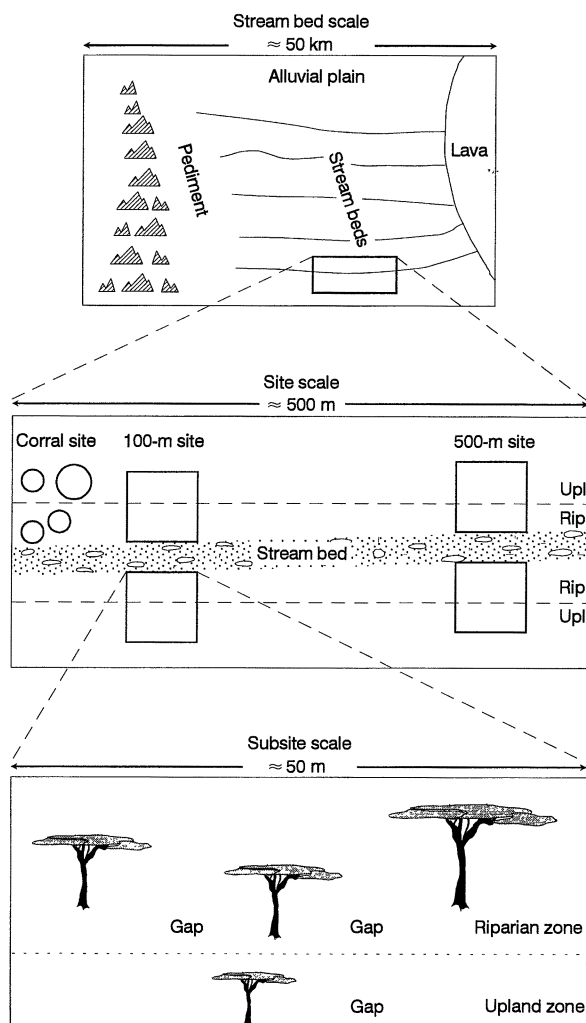On each stream bed, the influence of livestock corrals

FIG. 4. Schematic diagram of stream beds, sites, and subsites selected to study tree population dynamics. On each stream bed, three sites were established in corrals and 100 and 500 m from corrals; at each site, four subsites were chosen in riparian gaps, upland gaps, and under riparian and upland trees.

on tree recruitment was evaluated for four periods of the life cycle of *A. tortilis*: (1) seed distribution, (2) seedling emergence, (3) seedling survival and growth, and (4) survival and growth of older trees. Seed distribution and seedling emergence were measured for one cohort (1988), seedling density, survival, and growth for two cohorts (1987 and 1988), and older tree survival and growth for 12 other cohorts ranging from 2 to 39 yr in age.

The effects of livestock corrals on recruitment processes were investigated by establishing three types of sites (site scale, Fig. 4) on each stream bed for the 1988 cohort: one in corrals and two in noncorral sites. Corral sites were established in recently abandoned corrals (containing seeds or seedlings of the 1987 and 1988 cohorts); these were easily distinguished from surrounding areas by dark, circular patches of dung and decomposing thorn fencing. These sites were established only at abandoned homesites occupied during the dry season; only corrals at these homesites contained seeds or seedlings because seeds were only produced and consumed in the dry season. Corrals contained seeds deposited in only 1 yr, because homesites are occupied for only a few months (McCabe 1985). Corral sites were selected randomly from all the corrals found along each stream bed that contained seeds or seedlings. Only goat/sheep and camel corrals supported *A. tortilis* tree stands; goat/sheep corrals were the focus of this study because they were more abundant.

Noncorral sites were established at 100 and 500 m distant from the selected corral sites, located so that they were at least 100 or 500 m from any homesite or corral that had been occupied within the last 5 yr. This site design was selected to examine the expected decrease in seed and seedling densities along a livestock-use gradient from high densities in corrals, to moderate densities in nearby 100-m sites, to low densities in distant 500-m sites. The 500-m sites were expected to reflect the background conditions of the ecosystem, with no influence from recently used homesites. The gradient was selected to represent only livestock use; there were no known differences in geomorphology, hydrology, soils, or vegetation along these gradients. Only corral and 100-m sites were studied for the 1987 cohort.

The two other variables, landscape position and tree cover, were included in the design as the third level in the nested hierarchy (1988 cohort, Fig. 3; subsite scale, Fig. 4). Landscape position may represent differences in groundwater availability and tree cover may depress *A. tortilis* survival (e.g., Smith and Shackleton 1988). Thus, at each of the three sites (corral, 100-m, and 500-m) on each of the stream beds, we attempted to establish subsites under riparian and upland trees and in riparian and upland gaps. However, we found very few corrals under trees (in only three riparian and two upland subsites, rather than five apiece) so the sample sizes were unequal. In this paper, we emphasize the

effects of corral on the recruitment of *A. tortilis* trees; in subsequent papers, we explore the influence of landscape position, tree cover, climate, and other factors on *A. tortilis* population dynamics (R. S. Reid and J. E. Ellis, *unpublished manuscript*).

The study was initiated too late in 1987 to investigate seed distribution or seedling emergence; we measured only growth and survival of established seedlings in 1987. Also, there were only four stream beds where recruitment in noncorral sites was sufficient for study; thus we designed the study as a paired corral/noncorral comparison with four pairs (1987 cohort, Fig. 3). Landscape position (riparian and upland) and tree cover (under canopies and in gaps) were distinguished only for corral sites and again in pairs.

Establishing the age of tree cohorts

The ages of several cohorts of older trees were determined so that we could compare survival and growth rates of corral and noncorral trees over time. *A. tortilis* forms tree rings in Turkana but these are difficult to count and not reliable as indicators of tree age beyond ≈10 yr (Wyant and Reid 1992). Therefore we estimated the age of trees by obtaining information from our research crew, with 8 yr experience in the area, and from information furnished by reliable Turkana informants. For trees 1–3 yr old, we identified known-age stands at abandoned Turkana homesites where our team had conducted previous research. We were able to estimate ages of young trees (1–3 yr) accurately from seedling size and morphology and from deterioration rates of abandoned houses and corral bush fencing. For older cohorts, we had Turkana herd owners identify homesites having corral trees where they could clearly remember the year they had lived at the site. Turkana memory for both location and time is excellent; most often they recalled sites where important events had occurred (e.g., a child was born, a marriage was celebrated, and other occasions). With the help of a Turkana event calendar (Leslie and Fry 1989), we were able to determine the year that the pastoral family had lived at each site. We assumed that the tree stands at these sites germinated in the rainy season immediately following abandonment of the homesite, as occurred during this study in 1987–1988 (Reid 1992).

Distribution of seeds

The presence of dense stands of trees in old corrals suggested that livestock were responsible for substantial seed redistribution. We compared seed density in corral and noncorral soils in 1988 to estimate the magnitude of this redistribution. At four of the five stream beds seed density was measured at each subsite within each site. For each corral subsite, a measured volume of the entire depth of the dung layer (usually 3–6 cm) was collected ($n = 7$ collections/site). At each noncorral subsite, samples were taken from the top 6 cm of soil because this was the maximum depth at which

seeds were found during preliminary surveys. All sub-sites were circular; methods of Skalski (1987) were used to randomly place collections. Each collection was sifted through a 2 × 2 mm sieve and trapped seeds were counted. Seed width varied from 5 to 8 mm at the narrowest point.

Seed density was measured just after seedlings emerged, thus seedling density (taken at the same sites) was added to seed density to estimate the total number of seeds before germination.

Rate and spatial patterns of seedling emergence

Observations in 1987 suggested that most *A. tortilis* seedlings regenerated in livestock corrals. This might occur if nearly all viable seeds are redistributed into corrals by livestock, or if conditions within corrals greatly enhance seedling germination. The first possibility was tested in 1988 by the seed distribution analysis. To test the second possibility, we measured seedling densities at all subsites and then compared percent emergence by dividing seedling densities by number of seeds/m² in the soil profile. Note that emergence was measured rather than germination; the former includes both germination (cotyledon emergence from the seed coat) and survival of the cotyledons until they first emerge through the surface of the soil.

Seedling density was measured using sampling units of different sizes in corrals (quadrats) and noncorral sites (belt transects) because of large differences in density. In the same corrals used for seed-bank measurements, seedling density was quantified by counting seedlings in 10, randomly placed, 0.25 × 1.0 m quadrats. Outside corrals, we randomly placed 20 paired riparian and upland belt transects (*n* = 10/landscape position) perpendicular to and beginning at the edge of the stream bed, with five pairs of transects on each side of the stream bed at each 100-m and 500-m site. Transect width was 1.5 m; the length of the riparian transect was determined by the width of the riparian vegetation (usually 10–30 m). The riparian and upland transects abutted each other and were the same length. All seedlings within these transects were counted and seedling density was calculated by dividing seedling number by transect area. On each belt transect, presence or absence of tree overstory cover was recorded for each seedling.

Survival and growth of young seedlings

Another explanation for the paucity of seedlings observed outside corrals is that corral environments enhanced tree survival and growth subsequent to seedling emergence. To examine corral influences on seedlings, we followed seedling survival and growth throughout the study period. In 1987, 25 seedlings in each corral were mapped at two, randomly located points along a line bisecting the corral in a random compass direction. In 1988, 50 seedlings were sampled at three randomly placed points (Skalski 1987).

In all noncorral sites, 25 (1987 cohort) or 50 (1988 cohort) seedlings were marked at each site in both riparian and upland zones (with some under trees and some in gaps) along the randomly placed belt transects used to measure seedling densities. If more than the required number of seedlings were found along the transects, seedlings were chosen randomly from those found; otherwise, an intensive systematic search was made to locate additional seedlings to complete the sample.

At all sites we mapped each seedling and measured seedling height (from the root collar to the highest point in the canopy), two perpendicular canopy diameters (for calculations of canopy area), basal stem diameter of all stems just above the basal swelling, and number of branches and ground-level stems. An aggregate basal stem diameter was calculated by summing the areas (calculated from the diameters) of all stems and converting the summed area back into an aggregate diameter. This measure is strongly correlated with above-ground biomass in *A. tortilis* (Coughenour et al. 1990*c*). Consequently aggregate stem diameter was selected among the size parameters to represent a mean of relative growth rate (RGR) per day by the following equation (Harper 1977):

$$RGR = [\ln(\text{stem diameter}_{time2}) - \ln(\text{stem diameter}_{time1})]$$
$$\div (time2 - time1)$$

Seedlings were measured in August (early-dry season) and November (mid-dry) 1987, and in March (late-dry), May–June (mid-wet), and October (mid-dry) 1988. The 1988 seedlings were measured on the last two dates; 1987 seedlings were measured on all five dates. Neither stem diameter nor canopy area were recorded in August 1987. New individuals were substituted for marked seedlings that had died since the last sample date to maintain sample sizes.

Site selection and methods—survival and growth of older trees

Even though corrals might initially enhance seedling survival and/or growth, mortality rates might ultimately be higher or growth rates lower in corral stands than in noncorral stands due to crowding. Thus, older tree survival and growth were compared in 16 paired corral and noncorral sites, representing nine different cohorts (older cohorts, Fig. 3). Paired sites were either in riparian or upland areas, resulting in 12 upland and 4 riparian paired sites. For most cohorts, we were able to find a single example. However, for two cohorts (1975 and 1981) we found three sites, and for one cohort (1982) we found six. Thus, a total of 12 cohorts were studied at 21 different sites.

At each site, we mapped 25 trees, or all trees if there were fewer than 25, so trees could be relocated on subsequent sampling dates. Corral trees were selected for mapping by marking the 25 trees closest to a randomly placed line bisecting the corral. Noncorral trees

were selected from the trees clustered around the corral; these trees most likely germinated at the same time as the corral trees.

For the survival and growth portion of the study, we marked the 25 noncorral trees nearest to the edge of a 3-m band drawn around the corral. Only trees beyond the band were included to ensure that corral dung had not influenced them. Survival and growth measurements began in November 1987, for most corral stands and in March 1988, for corral stands supporting very old trees and for noncorral stands. Older trees were measured in the same manner and at the same time as seedlings.

To estimate tree density in noncorral sites, we used the 500-m sites instead of the areas just outside corrals. We chose the 500-m sites because they appeared to be relatively unaffected by recent human and livestock activities in comparison to the dense stands of trees growing very close to corrals. We then compared corral tree densities with the density of trees of the same size range at the 500-m sites.

Density at the 500-m sites was measured in adjacent, 5×20 m plots, oriented with the long side parallel to the stream bed and with the riparian plot on the stream edge. Upland plots were adjacent and contiguous to riparian plots. The number of plots sampled at each of the 5 stream beds was determined by the density of trees; additional plots were established and sampled until at least 100 trees were counted in both riparian and upland zones.

Data analysis

The seed and seedling study was replicated at the subsite level rather than the tree level because we wanted to avoid confounding location with subsite (Hurlbert 1984). Thus, each replicate was the mean response of 25–50 seedlings at each subsite.

Analyses were conducted with fixed-effects ANOVAs and preplanned comparisons made with t tests. The ANOVA main effects were site (corral, 100, and 500 m), landscape position (riparian, upland), and tree cover (under trees, in gaps). Stream beds were used as a blocking variable in the 1988 cohort analysis but when it was not significant ($P > 0.60$), it was dropped. We pooled the two noncorral sites (100 and 500 m) when results consistently showed no difference. $\text{Log}_{10}(x + 1)$ transforms were used for size and growth variables and an arcsine transform for proportion surviving; untransformed means were used for data presentation.

Most sites with older (2–39 yr) tree cohorts were not replicated within a cohort, thus paired inside and outside sites for each cohort and location were compared with G tests (Sokal and Rohlf 1981) for proportion surviving and t tests for growth variables. This nonreplication means that differences between corral and noncorral sites could be attributed to site characteristics not related to corral effects; however, consistent pat-
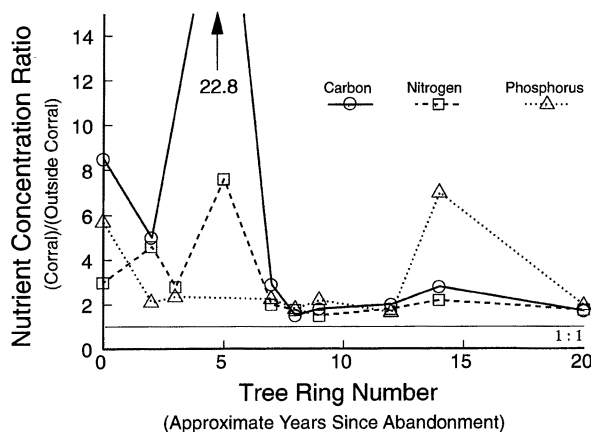

FIG. 5. Ratio of the concentration of nutrients in corral and noncorral soils. Tree ring number is closely correlated with age for young trees (Wyant and Reid 1992).

terns across many paired sites would imply corral effects.

RESULTS

Soil nutrients and moisture

The soils of the study area were low in nutrient content. Analyses of noncorral soils revealed that soil C, N, and P were 0.1%, 0.04% and 6 μg/g, respectively. By contrast, soils from abandoned livestock corrals, fertilized by massive inputs of dung and urine, contained significantly ($P < 0.001$) greater concentrations of nutrients (Fig. 5, J. E. Ellis et al., *unpublished data*). Soils from corrals with young tree seedlings contained nine times more C, three times more N, and six times more P than adjacent noncorral soils, and soil C and N remained 3–23× higher for 5 yr after corral abandonment. Thus soil nutrient availability was much higher for corral than noncorral seedlings for up to 5 yr, and nutrient values of corral soils remained twice those of background soils for at least 20 yr.

Corral soils also retained more moisture than noncorral soils. Surface dung contained more than double the moisture of surficial noncorral soils immediately after rain (28 vs. 13% water content, $P < 0.05$, Fig. 6a) and the soil wetting front infiltrated more deeply (at $P < 0.10$) in corral soils (37.3 ± 6.5 cm, mean $\pm$ 1 SE) than in adjacent noncorral soils (24.6 ± 3.2 cm) after rain. This suggests that the highly organic corral soils may have been more effective at preventing runoff and therefore trapped more rain than noncorral soils. Surface dung dried rapidly in corrals and was completely dry following 15 d without rain (Fig. 6a). However, the deep (50 cm) soils of corrals remained significantly wetter than noncorral soils 15 d after rainfall ($P < 0.05$). No other comparisons of corral and noncorral soils by depth were significantly different.

In the dry-down experiment, all soils were wetted to field capacity; therefore there was no chance for the dung-covered soils to sequester more water than the soils
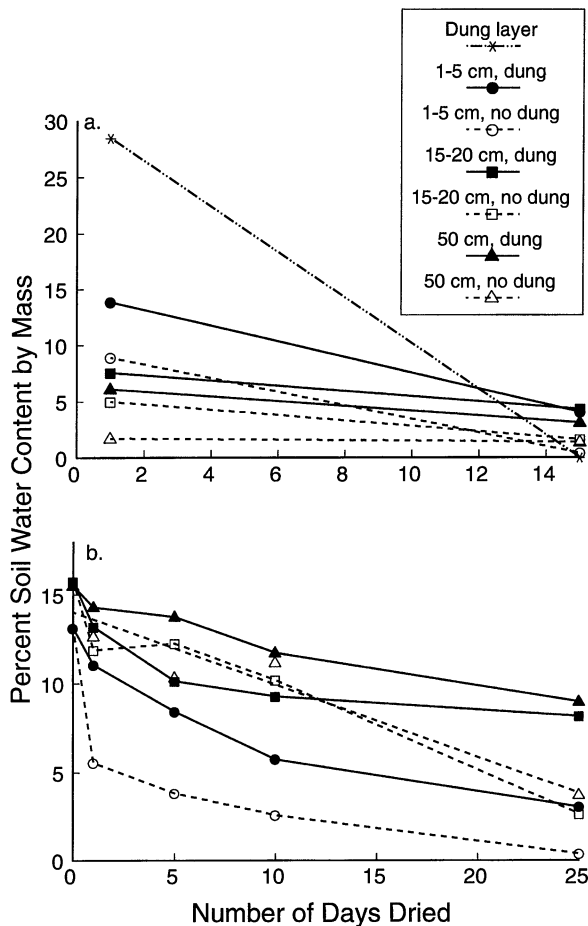
FIG. 6. Percent soil water content inside (dung) and outside (no dung) corrals (a) and in a drying experiment (b) at different depths over 1–15 or 1–25 d drying periods.

cover lost 58% of total water content compared with a 16% loss in dung-covered soils. The surficial soils with no dung appeared drier than dung-covered soils after 10 and 25 d, with differences approaching significance (P = 0.06 and 0.07, respectively).

Distribution of seeds

Analysis of seed distribution in 1988 confirmed that livestock dramatically influenced seed distribution and that corrals were strong loci for concentration of A. tortilis seed on the landscape. Mean seed density was, on average, over 85 times greater in corral than noncorral sites (P < 0.0001) with densities exceeding 6700 seeds/m² in some corrals (Table 1). However, seeds were still ubiquitous, although thinly distributed throughout the ecosystem; seeds were found at all sample sites.

This study was designed with the expectation that seed density would be greatest in corrals, moderate at 100-m sites, but that by 500-m distance, there would be no detectable effect of livestock on seed distribution. Seed density was 72% greater at 100-m than 500-m sites. However, high variation in seed densities caused this difference to be insignificant (P = 0.28); our hypothesis was not supported (Table 1).

Rate of seedling emergence

More seeds produced seedlings (=emergence rate) inside than outside corrals at three of four subsites (P < 0.0001, Fig. 7). The 100-m and 500-m noncorral sites averaged ≈1% emergence with no significant difference between these sites (P = 0.69). Emergence rates in corrals ranged from ≈2 to 15% and averaged about seven times the emergence rate of the noncorral sites overall. Thus, above and beyond the simple effects of seed concentration within corrals, something about the corral seeds themselves or about the physical environment of the corral, or both, enhanced seedling emergence.

However, field observations suggested that the depth of dung in corrals negatively affected emergence of

without dung, as probably happened in the field measurements. Nevertheless, the same patterns emerged as in the field analysis; surface soils without dung cover were significantly drier than dung-covered soils (P = 0.004, Fig. 6b). In 24 h, surficial soils without dung

TABLE 1. The number of seeds/m² and seedlings/100 m² (mean ± 1 SE) at corral and noncorral (100- and 500-m) sites, distinguishing among subsites in riparian and upland zones, and under trees and in gaps.

Subsite type	Sites*		
	Corral	100-m	500-m
	Seeds/m²		
Riparian tree	4501.6 ± 2944.2	131.1 ± 42.8	112.3 ± 31.9
Riparian gap	6728.3 ± 3662.3	37.6 ± 16.7	18.8 ± 8.3
Upland tree	140.6 ± 10.6	24.6 ± 15.6	8.3 ± 5.2
Upland gap	1195.6 ± 220.0	12.6 ± 3.1	10.2 ± 5.1
	Seedlings/100 m²		
Riparian tree	14556.0 ± 2831.6	45.6 ± 18.2	58.1 ± 24.5
Riparian gap	10928.0 ± 6320.2	18.5 ± 9.0	35.8 ± 29.4
Upland tree	2100.0 ± 140.0	15.9 ± 12.3	9.2 ± 7.5
Upland gap	4582.2 ± 1101.3	5.4 ± 1.7	1.8 ± 0.9

*Corral densities were all greater than noncorral densities within subsites; 100 and 500 m densities were not different, P < 0.001.
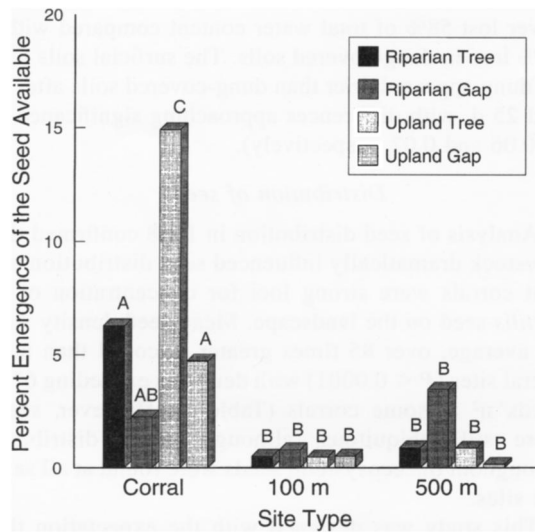
FIG. 7. Percent emergence in corral, 100-, and 500-m sites, differentiating among subsites. Bars topped with the same letter are not significantly different.

seedlings in some cases. When analyzed as a covariate in the ANOVA, dung depth was significant at $P < 0.10$. Percent emergence dropped when dung was deeper than 5 cm; dung of this depth was found in every third corral sampled. Dung depth is probably a function of the time a corral is occupied by livestock; therefore a corral that is occupied for a very long period (average time of occupance is ≈ 3 wk) may have a lower emergence rate than our results show.

Spatial and annual patterns of seedling densities, 1987 vs. 1988

Spatial patterns of seedling density paralleled spatial patterns of emergence: there were no differences in seedling densities between 100- and 500-m sites, but the combination of higher seed densities and greater emergence rates in corrals resulted in corrals supporting, on average, roughly 530 times as many seedlings per unit area as the 100- and 500-m noncorral sites ($P < 0.0001$, Table 1) in 1988. However, the corral vs. noncorral density difference was more dramatic in the normal rainfall year of 1987 than in 1988, when rainfall was 60% above average (Table 2). In August 1987, seedling density was roughly 9700 times greater in corrals than at noncorral sites where there appeared to be a near failure of successful establishment. This implies that the corral effect on tree recruitment is more pronounced in an average rainfall year, than in an above average year.

Survival and growth of young seedlings

The observed differences in seedling density between corral and noncorral sites resulted from greater seed density, higher emergence rates, and from enhanced survival of corral seedlings just after they emerged (Fig. 8a). Moreover, survival rates of 1988

TABLE 2. Mean ($\pm$ 1 SE) seedling densities of the 1987 and 1988 cohorts at corral and noncorral sites, sampled when seedlings were the same age (August 1987 and August 1988).

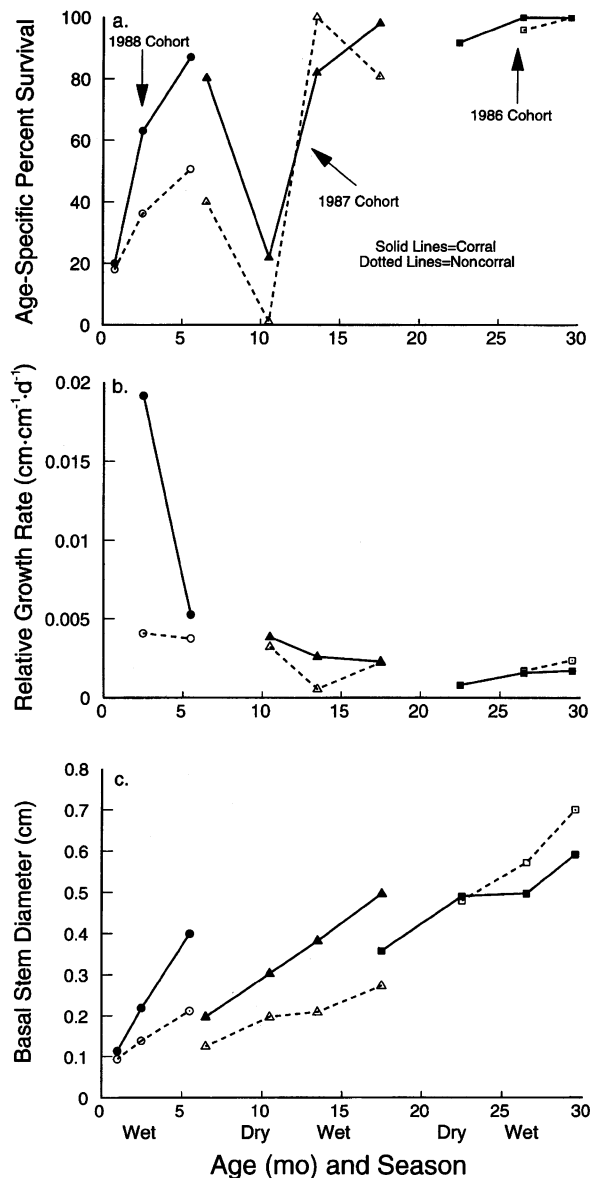| Landscape position	Year	Seedlings/100 m²	
		Corral sites	Noncorral sites
Riparian	1987	4272.4 ± 935.7	1.44 ± 0.71
	1988	2193.4 ± 504.2	17.03 ± 5.49
Upland	1987	8642.4 ± 838.1	0.45 ± 0.15
	1988	1471.8 ± 333.3	2.22 ± 0.95

FIG. 8. Age-specific survival (a), relative growth rate (b), and stem diameter (c) for three cohorts over 30 mo for corral and noncorral sites, averaged across subsites. Survival was measured separately for each sample period and sample periods were of unequal lengths. Germination (age 0) occurred at the beginning of May.

cohort seedlings continued to be greater inside than outside corrals ($P < 0.05$) through the first 6 mo of 1988.

Corral tree survival was also higher over the tree's first dry season for the 1987 cohort, although mortality rates were higher for both corral and noncorral trees during the dry season than for any other period assessed. This first dry season bottleneck was so severe that practically all noncorral seedlings on upland subsites died in 1987. By contrast, dry season seedling survival was about 16% for noncorral trees in the riparian subsite and 21% for all corral subsites. Following the first dry season, tree survival was uniformly high (80–100%) and similar for corral and noncorral trees up to 2.5 yr of age. Thus the advantages that corrals confer on trees are largely the result of processes taking place either prior to germination (seed distribution) or in the 1st yr of life. Nevertheless, the multiplicative effect of greater seed density, higher emergence rates, and greater early survival in corrals, together yield a population of young trees whose density is vastly greater inside than outside corrals.

The enhanced dry season survival rates of corral seedlings were, in part, related to their greater size. Size differences between corral and noncorral seedlings were initiated in the first 6 mo by increased relative growth rates inside corrals (Fig. 8b). These size differences were maintained well into the next year (Fig. 8c), although growth was significantly greater only for the first 6 mo. The greatest effect of corral environments on growth occurred in the first 2 mo, when growth was four times greater in corral than noncorral seedlings. Between 2 and 6 mo, growth was only 25% higher inside than outside corrals. After 27 mo, outside corral plants appeared to grow faster than those inside, as might be expected due to crowding in corrals.

Seedlings in the 1986–1988 cohorts were not the same size even when they were the same age. Stem diameters (Fig. 8c) attained by 1988 cohort seedlings at 5.5 mo were not attained by the 1987 and 1986 cohorts until 14 and 18 mo, respectively. These disparities followed rainfall patterns; mean annual rainfall at the Lodwar weather station, where long-term records are kept, was 60% above the 65-yr mean in 1988, near average in 1987, and 10% below average in 1986. Thus growth of young trees was related to annual rainfall.

Survival and growth of older trees

Despite the fact that corrals enhanced the survival and growth of younger trees, we expected the survival rates of older trees to be higher in noncorral than corral sites because of crowding. However, tree survival for cohorts ranging from 3 to 29 yr was uniformly high both inside and outside corrals (Table 3), with no significant differences between sites. Mortality in older trees was very low over this study period. However, a longer study period may reveal differential survival inside and outside corrals (research in progress).

Results of the size/growth comparison were equivocal. There were a few sites where corral and noncorral trees were of different size. At these sites, corral trees were always taller than noncorral trees (Table 3) and sometimes had larger stem diameters. Canopy area, by contrast, was larger in noncorral than corral trees at some sites. Noncorral trees also sometimes had more aboveground stems than corral trees. However, in the one cohort (1982, 6 yr old) where a large number of sites allowed a replicated comparison between corral and noncorral trees, there were no survival or growth differences (t test).

The density of older trees in corral and noncorral stands representing many different cohorts can be concatenated to create hypothetical survivorship curves for *A. tortilis* (Fig. 9). The curve for the corral stands accurately portrays the survivorship of the corral cohorts that we sampled. The curve for the noncorral stands is only generally representative of survivorship of these trees, because, unlike corral trees, we were not able to estimate the age of trees in noncorral stands with complete accuracy once trees exceeded 2 yr of age (see Methods). Inaccurate age estimation led to the obvious artifact in the survivorship curve for noncorral trees, showing an increase in density after 2 yr. Despite this shortcoming, the curves do display some interesting generalities. The overall shape of both curves is as expected: mortality is very high in young trees and low in older trees. But the slopes are different; noncorral stands initially appear to thin much more rapidly than corral stands, due to high mortality in the first 2 yr. The density of noncorral tree populations fell by two to three orders of magnitude in the first 2 yr, whereas corral populations fell by only one order of magnitude.

Mortality patterns in older trees, however, appear to switch. In corral stands, older trees appear to die at a fairly constant rate, even when trees are >10 yr old. This would be expected if corral stands, because of crowding, thin consistently over time. By contrast, older trees in noncorral stands show very little mortality after 10 yr, if any. This suggests that mortality is indeed somewhat higher in the crowded corral stands when trees are beyond 2–3 yr of age.

DISCUSSION

Redistribution of seeds and seedlings by livestock

Livestock and *A. tortilis* seeds are linked by a series of strong interactions. In Turkana, pods fall in the dry season (R. S. Reid and J. E. Ellis, *unpublished manuscript*) when other sources of forage are scarce and thus are highly attractive to livestock (Coppock et al. 1987). In other dry ecosystems, even though many of the seeds consumed by livestock are digested (Ahmed 1986), seeds that pass through the digestive tract intact become scarified and germinate at higher rates than noningested seeds (7 vs. 0%, Lamprey 1963; 13 vs. 1%,

TABLE 3.   Older tree survival for 7 mo (for corral and noncorral sites) and 12 mo (for corrals only) starting in March 1988, and size in March 1988. Most sites are paired corral and noncorral sites except some older sites.* Corral age is as of March 1988 (subtract corral age from 1988 to calculate germination year). C = corral sites, NC = noncorral sites, NT = not taken.

Site name	Landscape position	Corral age (yr)	7 (12)-mo survival		Stem diameter (cm)		Height (cm)		Canopy area (cm²)		Stem number	
			C	NC	C	NC	C	NC	C	NC	C	NC
Loyapachui	Upland	2	100.0 (100.0)	96.0	0.60	0.48	14.9	10.4	486.0	317.2	1.3	1.1
Kachalakeny	Upland	4	89.3 (71.4)	100.0	0.75	0.98	16.7	12.3	307.7	1134.5	1.2	3.0
Kadokochin	Upland	5	100.0 (100.0)	100.0	1.36	0.79	29.7	16.1	6062.5	914.0	1.2	2.6
Kochodin	Riparian	6	85.8 (85.8)	92.9	1.10	1.11	24.9	18.4	4425.0	2532.8	4.1	3.2
Kanaiki	Riparian	6	81.8 (72.0)	92.0	0.77	0.85	21.2	24.8	833.8	2211.6	2.9	3.4
Kalorigisia	Riparian	6	95.8 (91.8)	100.0	1.29	1.11	32.4	20.6	5458.3	4530.9	4.2	2.8
Kanaiki	Upland	6	62.2 (52.3)	92.2	1.10	1.25	22.3	27.5	1877.2	5285.3	4.1	3.8
Nachalal	Upland	6	93.5 (93.5)	100.0	1.10	1.28	22.5	26.8	3280.8	7762.8	2.8	3.6
Narr-doi	Upland	6	93.8 (93.8)	100.0	1.41	1.05	36.3	17.9	4519.6	2542.6	3.3	4.1
Kochodin	Riparian	7	92.0 (73.6)	96.0	0.86	0.94	18.3	20.0	1001.6	1068.1	3.8	2.9
Kochodin	Upland	7	100.0 (92.0)	100.0	0.93	0.91	17.2	15.1	2514.8	1973.6	4.0	3.5
Kaegilai	Upland	7	92.0 (92.0)	96.0	1.01	0.95	25.9	18.5	1872.2	1703.3	3.6	3.4
Moru-Ayket	Upland	8	100.0 (NT)	100.0	1.95	2.02	41.4	38.5	10 896.6	8736.9	3.4	3.5
Kalotiman	Upland	9	87.4 (83.9)	92.0	1.51	1.70	37.3	36.0	5947.1	7765.3	4.4	3.2
Loyapachui 1	Riparian	13	100.0 (NT)	NT	8.61	NT	303.8	NT	125 622.5	NT	2.1	NT
Loyapachui 2	Riparian	13	100.0 (NT)	NT	9.91	NT	433.1	NT	160 726.9	NT	1.9	NT
Loyapachui 3	Upland	13	100.0 (NT)	100.0	1.98	1.43	34.6	22.7	10 679.2	5364.2	3.8	3.5
Tamantan-awi	Riparian	26	100.0 (NT)	NT	13.07	NT	400.9	NT	203 200.2	NT	2.8	NT
Kalokeya	Riparian	27	100.0 (NT)	NT	6.47	NT	335.6	NT	91 791.6	NT	2.4	NT
Moru-Asimit	Upland	29	100.0 (NT)	94.4	12.06	11.24	309.4	382.8	216 691.4	150 110.3	3.3	2.1
Nachalal	Riparian	40	100.0 (NT)	NT	13.60	NT	455.0	NT	NT	NT	4.0	NT

* Only paired values that are underlined are significantly different comparing within a variable between corral and noncorral sites, $P < 0.01$, G test (survival) and t test (size).

Halevy 1974; 54 vs. 20%, Ahmed 1986). In addition, because passage through livestock takes several hours (Ahmed 1986), livestock disperse seed much farther from the parent tree than would occur otherwise. Furthermore, in Turkana, many seeds are deposited in nutrient- and moisture-rich patches of dung in livestock corrals.

The importance of these strong interactions between seedpods and livestock rests in part with the proportion of seeds consumed by ruminant herbivores each year. We did not measure seedpod consumption. However, our field observations and those of others (Halevy 1974, Lamprey et al. 1974) suggest that herbivores, when in their dry season range, may consume most of

the seedpods produced by *A. tortilis* trees. In Turkana, the ruminant herbivore guild is heavily dominated by livestock, with smaller populations of wild herbivores present (especially Grant's gazelles). Thus most of the seeds in both corrals and noncorral seed banks may have been first scarified by ruminant digestion.

Effect of corral environments on population processes

Corrals were not only an important locus of seed concentration on the landscape, but the corral environment increased the chance of emergence and enhanced survival. Soil moisture and nutrients were maintained longer in corral soils than in adjacent noncorral soils,
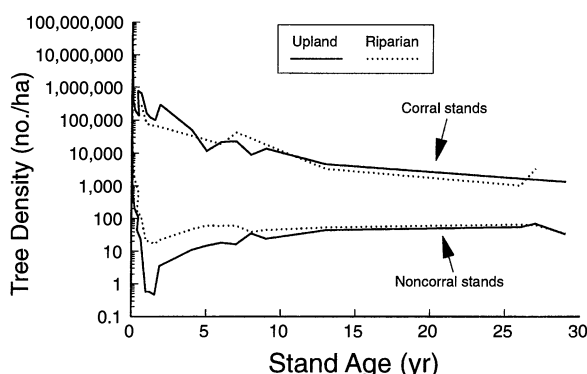
FIG. 9. Hypothetical survivorship curves for corral and noncorral trees created from tree density data (no./ha, log scale) in stands of different ages found in riparian and upland areas.

probably because dung and urine increased nutrients and reduced evaporation. Corral dung also facilitated deeper penetration of rainfall into the soil, allowing the recharge of subsoil water, which may be essential to woody plant survival (Walter 1979, Walker et al. 1981). Dung may prevent formation of runoff crusts commonly seen during heavy rains in dry ecosystems (Cheruiyot and Blackburn 1986), thus aiding infiltration.

The length of time the soil profile remains wet probably explains why more seedlings emerged in corrals than in noncorral sites. Seedling emergence rates are often positively correlated with the length of time the soil contains sufficient moisture to stimulate germination (e.g., Angevine and Chabot 1979, Augspurger 1979, Kadmon and Shmida 1990). However, an alternative explanation for the differences in emergence rates is that seed populations in corrals differ from those in noncorral sites. Corral seed populations probably consist of more seeds that have passed through a ruminant gut than populations outside corrals, although, as suggested above, this difference may not be great. Ingestion not only increases germination, but it also frequently destroys bruchid-infested seeds (Jarman 1976) that usually have little capacity to germinate (Halevy 1974, Lamprey et al. 1974). Hence, enhancement of emergence in corrals may result from both previous ingestion and differences between the corral and noncorral soils.

After seedling emergence, the corral environment continued to promote the survival and growth of young seedlings compared with noncorral soils. Survival is probably controlled by water availability because moisture stress is the most important seedling mortality agent in arid systems (Evenari et al. 1971, Fowler 1986, Soriano and Sala 1986, Grice and Westoby 1987) whereas growth differences may be the result of both increased nutrients and moisture. Even though soil moisture may influence vegetative growth more than nutrients in areas with very low rainfall (e.g., Breman

and de Wit 1983), much of 1st-yr growth of corral seedlings occurred in the wet season when water probably was not limiting. For short periods of water sufficiency, nutrients may become the major factor limiting growth.

Differences in initial growth rates meant that young corral seedlings were much larger than their noncorral counterparts. Greater size was likely responsible for increased survival rates in corral compared with noncorral seedlings; diminutive size probably explains why so few noncorral seedlings survived the dry season. Larger seedlings usually survive better than smaller ones (Weiner and Thomas 1986, Peet and Christensen 1987) because greater biotic resources allow larger seedlings to better endure environmental stress (Harper 1977) and to compete successfully if crowding occurs (Harper 1977, Peet and Christensen 1987).

As trees grow older and corral stands become more crowded, we would expect more mortality and slower growth in corrals than in noncorral stands. It appears that mortality may indeed be greater in corral than noncorral stands. However, there is no evidence that crowded corral trees grew more slowly; in fact, when there was a difference in stem diameters (and thus biomass, Coughenour et al. 1990c), older corral trees were larger than noncorral trees of the same age. This implies that the increased moisture and nutrients in corrals promote growth and possibly survival of trees over long periods.

Interactions between corral environments and rainfall

Turkana pastoralists live in a highly pulsed environment that exhibits discontinuous or nonequilibrial dynamics (Ellis and Swift 1988). Ecologists have long recognized that woody plant establishment is highly variable in arid ecosystems like Turkana, occurring as a series of unpredictable, discontinuous events, often during unusual years with high rainfall (Harper 1977). In more mesic and less variable systems, establishment sometimes occurs every year. Recruitment of trees in noncorral sites is a striking example of a discontinuous pattern, especially in upland sites; the success of recruitment varies widely depending primarily on annual rainfall. However, recruitment in livestock corrals is entirely different; here, successful recruitment appears to be only loosely coupled to the magnitude of rainfall. Increased nutrients and moisture in corrals not only increase recruitment but shift recruitment patterns from pulsed and discontinuous toward more regular and continuous. This stabilization of A. tortilis population dynamics may indicate that corral environments provide the means for a portion of the population to cross a threshold to a new transitional state (e.g., Westoby et al. 1989, Friedel 1991). This also suggests that this system may be less abiotically driven than proposed (Ellis and Swift 1988).

The problem of maintaining persistence in nonequi-

librial ecosystems has been addressed from both theoretical and practical perspectives. When systems are destabilized by strong external forces, model analyses show that stabilization can be achieved either by increasing the spatial scale of the model universe or by resource substitution or compensation (DeAngelis and Waterhouse 1987). These are exactly the stabilizing strategies that nomadic pastoralists pursue in the face of severe destabilizing droughts (Ellis and Swift 1988). The results of the present study show that yet a third strategy exists, which stabilizes population processes under nonequilibrial conditions. The actions of pastoralists and livestock stabilize the population processes of *A. tortilis* by concentrating resources (nutrients and water) together with propagules in a small spatial domain (the corral) where growing conditions are much improved over those of the background ecosystem. The stabilization effect of these concentration zones is not unlike that of valley bottomlands in many arid ecosystems (Scoones 1991). Because corrals change location frequently, the resource concentration is not, in the long run, site specific but influences a large portion of the total ecosystem. We propose that the principle of "temporary resource concentration" may be considered as an additional means, along with resource substitution and expanding spatial scales, to stabilize population (or ecosystem) dynamics under nonequilibrial conditions.

Potential impacts of pastoralists on dry woodlands

Years of observation and sound reasoning have led scientists and managers to conclude that pastoralists and their livestock, through overuse of communal vegetative resources (e.g., Hardin 1968), often have highly negative impacts on arid ecosystems (Pratt and Gwynne 1977, Lamprey 1983, Sinclair and Fryxell 1985). This is certainly the case near villages and towns in Turkana, where human and livestock densities are relatively high. However, our calculations show that most of the Turkana landscape is more thinly populated with >95% of the land area at least 5 km from a settlement. In these areas, pastoralist land-use practices make *A. tortilis* recruitment more reliable, and may enhance tree population sizes. This phenomenon adds strength to recent theoretical and empirical evidence (Ellis and Swift 1988, Westoby et al. 1989, Binns 1990, Hellden 1991, Behnke and Scoones 1993) that suggests we need to rethink our generalizations about how pastoralists and livestock affect arid ecosystems.

The process represented by pastoralist stabilization of tree recruitment has important implications for rangeland management in these systems. First, if patches of dung, like those found in corrals, can make recruitment more reliable, it is an agroforestry technique that needs to be further investigated for these systems where wood is often in short supply. The materials for this dung mulching are easily available and *A. tortilis*

is preadapted to arid ecosystems, requiring little additional nutrients and water to be successful. Second, policy-makers and managers might reconsider assumptions that pastoralists cause pervasive negative impacts; when allowed to operate opportunistically and move freely in rangelands (e.g., Sanford 1983), pastoralists may have minimal negative or even positive impacts on tree populations. Development strategies that enhance movement and opportunism may be the most ecologically sustainable (Behnke and Scoones 1993). Lastly, development programs that seek to settle mobile pastoralists like the Turkana may alter the recruitment rates and population patterns of *A. tortilis*. Where this species is an important component of the plant community, such tree population changes could alter the structure of landscapes and ecosystems in unanticipated ways.

All the same, are pastoralist-livestock-tree interactions widespread or is this a rare, unimportant phenomenon, restricted to South Turkana? *Acacia* trees were observed in abandoned corrals built by Maasai pastoralists over 30 yr earlier (Lamprey 1963) and can be seen in abandoned pastoral homesites in southern Ethiopia (M. Atsedu, *personal communication*) and southern Kenya (R. S. Reid, *personal observation*). In southern Africa, patches of *A. tortilis* on nutrient-rich soil have been found on Iron Age Tswana settlements in the middle of nutrient-poor *Burkea* savanna (Walker and Noy-Meir 1982, Blackmore et al. 1990, Scholes 1990). These researchers hypothesized that the rich patches have been maintained by preferential use of the nutrient-rich *Acacia* by herbivores, but they appear not to have asked how the patches came to have an entirely different tree species composition than the surrounding savanna in the first place. It is possible that these patches originated in Iron Age Tswana livestock corrals. If so, this suggests that livestock may have affected tree recruitment in some African environments not just for the past few decades but for hundreds of years.

LITERATURE CITED

Ahmed, A. El Houri. 1986. Some aspects of dry land afforestation in the Sudan with special reference to *Acacia tortilis* (Forsk.) Hayne, *A. senegal* Willd. and *Prosopis chilensis* (Molina) Stuntz. Forest Ecology and Management **16**:209–221.
Angevine, M. W., and B. F. Chabot. 1979. Seed germination

syndromes in higher plants. Pages 188–206 *in* O. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, editors. Topics in plant population biology. Columbia University Press, New York, New York, USA.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist **134**:545–561.

Augspurger, C. K. 1979. Irregular rain cues and the germination and seedling survival of a Panamanian shrub (*Hybanthus prunifolius*). Oecologia **44**:53–59.

Behnke, R. H., and I. Scoones. 1993. Rethinking range ecology: implications for rangeland management in Africa. Pages 1–30 *in* R. H. Behnke, I. Scoones, and C. Kerven, editors. Range ecology in disequilibrium. Overseas Development Institute, London, England.

Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology **26**:1005–1024.

Bernard-Reversat, F. 1982. Biogeochemical cycle of nitrogen in a semi-arid savanna. Oikos **38**:321–332.

Binns, T. 1990. Is desertification a myth? Geography **75**:75–113.

Blackmore, A. C., M. T. Mentis, and R. J. Scholes. 1990. The origin and nature of nutrient-enriched patches within a nutrient-poor savanna. Journal of Biogeography **17**:463–470.

Breman, H., and C. T. de Wit. 1983. Rangeland productivity and exploitation in the Sahel. Science **221**:1341–1347.

Charney, J. G., P. H. Stone, and W. J. Quirk. 1975. Drought in the Sahara: a biophysical feedback mechanism. Science **187**:434–435.

Cheruiyot, S. K., and W. H. Blackburn. 1986. Effects of *Panicum maximum* and *Digitaria macroblephara* on water infiltration. Pages 201–208 *in* R. M. Hansen, B. M. Woie, and R. D. Childs, editors. Proceedings of the Conference of the Agricultural Research Center, Egerton College, April 1986. Njoro, Kenya.

Coppinger, K. 1987. Geomorphic control of distribution of woody regeneration and soil moisture in Turkana District, Kenya. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Coppock, D. L., J. E. Ellis, and D. M. Swift. 1986. Livestock feeding ecology and resource utilization in a nomadic pastoral ecosystem. Journal of Applied Ecology **23**:573–583.

Coppock, D. L., J. E. Ellis, and D. M. Swift. 1987. Seasonal food habits of livestock in South Turkana, Kenya. East African Agricultural and Forestry Journal **52**:196–207.

Coughenour, M. B., D. L. Coppock, and J. E. Ellis. 1990*b*. Herbaceous forage variability in an arid pastoral region of Kenya: importance of topographic and rainfall gradients. Journal of Arid Environments **19**:147–159.

Coughenour, M. B., D. L. Coppock, M. Rowland, and J. E. Ellis. 1990*a*. Dwarf shrub ecology in Kenya's arid zone: *Indigofera spinosa* as a key forage resource. Journal of Arid Environments **18**:301–312.

Coughenour, M. B., and J. E. Ellis. 1993. Landscape and climatic control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. Journal of Biogeography **20**:383–398.

Coughenour, M. B., J. E. Ellis, and R. G. Popp. 1990*c*. Morphometric relationships and developmental patterns of *Acacia tortilis* and *Acacia reficiens* in Southern Turkana, Kenya. Bulletin of the Torrey Botanical Club **117**:8–17.

Coughenour, M. B., J. E. Ellis, D. M. Swift, D. L. Coppock, K. A. Galvin, J. T. McCabe, and T. C. Hart. 1985. Energy extraction and use in a nomadic pastoral ecosystem. Science **230**:619–625.

DeAngelis, D. L., and J. C. Waterhouse. 1987. Equilibrium and non-equilibrium concepts in ecological models. Ecological Monographs **57**:1–21.

Dodd, J. L. 1994. Desertification and degradation in sub-Saharan Africa. Bioscience **44**:28–34.

Ellis, J. E. 1994. Ecosystem dynamics and economic development of African rangelands: theory, ideology, events and policy. Pages 174–185 *in* S. Breth, editor. Reinventing agriculture and rural development. Winrock International, Morrilton, Arkansas, USA.

Ellis, J. E., D. L. Coppock, J. T. McCabe, K. Galvin, and J. Weinpahl. 1984. Aspects of energy consumption in a pastoral ecosystem: wood use by the South Turkana. Pages 164–187 *in* C. Barnes, J. Ensminger, and P. O'Keefe, editors. Energy, environment and development in Africa. Volume 6 of Wood, energy and households: perspectives on rural Kenya. Beijer Institute and the Scandinavian Institute of African Studies, Stockholm and Uppsala, Sweden.

Ellis, J. E., M. B. Coughenour, and D. M. Swift. 1991. Climate variability, ecosystem stability and implications for range and livestock development. Pages 1–12 *in* R. Cincotta, C. Gay, and G. Perrier, editors. New concepts in international rangeland development. Theories and applications. Proceedings, International Rangeland Symposium. Washington, D.C., USA.

Ellis, J. E., K. Galvin, J. T. McCabe, and D. M. Swift. 1987. Pastoralism and drought in Turkana District, Kenya. A report to the Norwegian Agency for International Development (NORAD), Nairobi, Kenya.

Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. Journal of Range Management **41**:450–459.

Evenari, M., L. Shannan, and N. Tadmor. 1971. The Negev: the challenge of a desert. Harvard University Press, Cambridge, Massachusetts, USA.

Forse, B. 1989. The myth of the marching desert. New Scientist **4**:31–32.

Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist **115**:131–145.

Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management **44**:422–426.

Galvin, K. 1985. Food procurement, diet and nutrition of Turkana pastoralists in the ecological and social context. Dissertation. State University of New York, Binghamton, New York, USA.

Grice, A. C., and M. Westoby. 1987. Aspects of the dynamics of the seed-banks and seedling populations of *Acacia victoriae* and *Cassia* spp. in arid western New South Wales. Australian Journal of Ecology **12**:209–215.

Halevy, G. 1974. Effects of gazelles and seed beetles (Bruchidae) on germination and establishment of *Acacia* species. Israel Journal of Botany **23**:120–126.

Hardin, G. 1968. Tragedy of the commons. Science **162**:1243–1248.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, England, UK.

Hellden, U. 1991. Desertification—time for an assessment? Ambio **20**:372–383.

Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–211.

Jarman, P. J. 1976. Damage to *Acacia tortilis* seeds eaten by impala. East African Wildlife Journal **14**:223–225.

Kadmon, R., and A. Shmida. 1990. Patterns and causes of spatial variation in the reproductive success of a desert annual. Oecologia **83**:139–144.

Lamprey, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. East African Wildlife Journal **1**:63–93.

————. 1983. Pastoralism yesterday and today: the over-grazing problem. Pages 643–666 *in* F. Bourlière, editor. Tropical savannas: ecosystems of the world. Volume 13. Elsevier, Amsterdam, The Netherlands.

Lamprey, H. F., G. Halevy, and S. Makacha. 1974. Inter-actions between *Acacia* bruchid seed beetles and large her-bivores. East African Wildlife Journal **12**:81–85.

Le Houérou, H. N. 1980. The role of browse in the man-agement of natural grazing lands. Pages 329–338 *in* H. N. Le Houérou, editor. Browse in Africa. International Live-stock Centre for Africa, Addis Ababa, Ethiopia.

————. 1989. The grazing land ecosystems of the African Sahel. Ecological Studies Number 75. Springer-Verlag, Berlin, Germany.

Leslie, P. W., and P. H. Fry. 1989. Extreme seasonality of births among nomadic Turkana pastoralists. American Jour-nal of Physical Anthropology **79**:103–115.

Little, M. A., and B. R. Johnson. 1984. Appendix I: weather conditions in South Turkana, Kenya. Pages 298–314 *in* R. Dyson-Hudson and J. T. McCabe, editors. Turkana nomad-ism: coping with an unpredictably varying environment. Human Relations Files, New Haven, Connecticut, USA.

Maranga, E. K. 1986. An ecological perspective of the phy-tosociology of woody Acacia/herbaceous-understory com-plex. Pages 243–252 *in* R. M. Hansen, B. M. Woie, and R. D. Childs, editors. Proceedings of the Conference of the Agricultural Research Center, Egerton College, April 1986. Njoro, Kenya.

McCabe, J. T. 1985. Livestock management among the Tur-kana: a social and ecological analysis of herding in an East African pastoral population. Dissertation. State University of New York, Binghamton, New York, USA.

Patten, R. P. 1991. Pattern and process in an arid tropical ecosystem: a landscape analysis of Ngisonyoka Turkana, Kenya. Dissertation. Colorado State University, Fort Col-lins, Colorado, USA.

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. Bioscience **37**:586–594.

Pratt, D. J., and M. D. Gwynne. 1977. Rangeland manage-ment and ecology in East Africa. Hodder and Stoughton, London, England.

Reid, R. S. 1992. Livestock-mediated tree regeneration: im-pact of pastoralists on dry tropical woodlands in Africa. Dissertation. Colorado State University, Fort Collins, Col-orado, USA.

Sanford, S. 1983. Management of pastoral development in the Third World. John Wiley and Sons, Chichester, En-gland, UK.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. K. Huenneke, W. M. Jarrrell, R. A. Virginia, and W. G. Whit-ford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Scholes, R. J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. Journal of Bio-geography **17**:415–419.

Scoones, I. 1991. Wetlands in drylands: key resources for agricultural and pastoral production in Africa. Ambio **20**: 366–371.

Sinclair, A. R. E., and J. M. Fryxell. 1985. The Sahel of Africa: ecology of a disaster. Canadian Journal of Zoology **63**:987–994.

Skalski, J. R. 1987. Selecting a random sample of points in circular field plots. Ecology **68**:749.

Smith, T. M., and S. E. Shackleton. 1988. The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. South African Journal of Botany **54**:375–379.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, San Francisco, California, USA.

Soriano, A., and O. E. Sala. 1986. Emergence and survival of *Bromus setifolius* seedlings in different microsites of a patagonian arid steppe. Israel Journal of Botany **35**:91–100.

Stebbings, E. P. 1935. The encroaching Sahara: the threat to West Africa colonies. Geographical Journal **86**:506–524.

Steppler, H. A., and P. K. Nair. 1987. Agroforestry: a decade of development. International Council for Research in Agroforestry, Nairobi, Kenya.

Tolsma, D. J., W. H. O. Ernst, R. A. Verwey, and R. Vooijs. 1987. Seasonal variations of nutrient concentration in a semi-arid savanna ecosystem in Botswana. Journal of Ecol-ogy **75**:755–770.

Tucker, C. J., H. E. Dregne, and W. W. Newcomb. 1991. Expansion and contraction of the Sahara Desert from 1980 to 1990. Science **253**:299–301.

UNEP. 1991. Status of desertification and implementation of the United Nations plan of action to combat desertification. Draft report. United Nations Environment Programme, Nai-robi, Kenya.

Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. Jour-nal of Ecology **69**:473–498.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556–590 *in* B. J. Huntley and B. H. Walker, editors. Ecology of tropical savannas. Springer-Verlag, Berlin, Germany.

Walter, H. 1979. Vegetation of the earth and ecological sys-tems of the geo-biosphere. Springer-Verlag, New York, New York, USA.

Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos **47**:211–222.

Weltzin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. Journal of Vegetation Science **1**:325–334.

Westoby, M. B., B. H. Walker, and I. Noy-Meir. 1989. Op-portunistic management for rangelands not at equilibrium. Journal of Range Management **42**:265–274.

Wyant, J. G., and J. E. Ellis. 1990. Compositional patterns of riparian woodlands in the Rift Valley of northern Kenya. Vegetatio **89**:23–37.

Wyant, J. G., and R. S. Reid. 1992. Determining the age of *Acacia tortilis* with ring counts for South Turkana, Kenya: a preliminary report. African Journal of Ecology **30**:176–180.