

Plant-soil interactions in primary succession at Hawaii Volcanoes National Park

Pamela Matson

Ecosystem Science and Technology Branch, NASA-Ames Research Center, Moffett Field, CA 94035, USA

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Summary. Plant nutrient status and physiological processes were examined in relation to soil nutrient characteristics under individuals of five species colonizing a young cinder deposit in Hawaii Volcanoes National Park. Two exotic species, *Buddleja asiatica* and *Myrica faya*, had high photosynthetic rates and high nitrogen concentrations and relatively easily decomposed leaves; soils under them had high concentrations of nitrogen, cations, and organic matter and high rates of net nitrogen mineralization. At the other extreme, the natives *Metrosideros polymorpha* and *Vaccinium reticulatum* had low plant concentrations and photosynthetic rates, and low concentrations and turnover rates of N in the soil. Thus, a strong correlation exists between soil processes and plant processes, suggesting a positive feedback cycle.

Key words: Plant-soil interactions – Nutrient cycling – Nitrogen fixation – Decomposition – Primary succession

The reciprocal influences of plants and soil are a major factor structuring community composition and soil properties. These interactions, however, are often difficult to examine because the complex history of vegetation and soil development in many sites inhibits an understanding of cause and effect relationships (Bazzaz 1983). One of the best situations in which to study such interactions is during early primary succession. Early sparse colonization on a relatively homogenous substrate allows individual plant-soil interactions to be examined in isolation from other longer-term effects. In this study, plant nutrient status and physiological processes were examined in individuals of five species colonizing a young ash deposit in Hawaii Volcanoes National Park; soil nutrient concentrations and processes under individuals of each species were also measured and related to plant processes.

Study site

This research was carried out in Hawaii Volcanoes National Park (HAVO), near the summit (1250 m) of Kilauea Volcano (19° 20' N, 155° 15' W) on the island of Hawaii. Annual precipitation in the area is approximately 2400 mm; mean annual temperature is 16° C. Measurements were carried out in the Devastation Trail area that was buried in 1 to 3 m of cinder during a 1959 eruption of Kilauea Iki. It is now an open site sparsely colonized by several native species, including *Metrosideros polymorpha*, *Vaccinium reticulatum*, and *Dubautia scabra*. Several exotic species are also invading the area; among the most important of these are *Buddleja asiatica* and *Myrica faya* (an actinorrhizal N fixer).

Plant growth on this substrate is limited by nitrogen; no other nutrient elicits a growth response in *Metrosideros* (Vitousek et al. 1987). Because of this strong N limitation, a comparison of the soil-plant processes of the actinorrhizal N-fixer *Myrica faya* with the non-fixers was of special interest.

Methods

Soil characteristics and processes

In April 1986, cinder (0–15 cm depth) was collected from two points beneath the canopy of 10 individuals of *Metrosideros*, *Dubautia*, *Vaccinium*, *Buddleja*, and *Myrica*. Individuals were selected on the basis of isolation from other plants; *Vaccinium* and *Dubautia* individuals were less than 1 m tall, *Buddleja* were 1–2 m tall, and *Myrica* and *Metrosideros* were 1–2.5 m tall. The two soil cores per plant were composited, hand sieved to remove rocks and plant material > 10 mm in diameter, and returned to the laboratory at HAVO for processing. Ten samples of soil were also collected from open areas without vegetation or any obvious decomposing plant material.

Within 6 h after collection, subsamples of fresh soil were placed in cups for a number of analyses. For measurement of inorganic N concentrations, two 20 g subsamples of each sample received 100 mL of 2N NaCl and were vigorously shaken. After 18–24 h, the supernatant was removed and returned to Ames Research Center (ARC) for analysis. Nitrate-N and ammonium-N concentrations in

the supernatant were analyzed colorimetrically (Technicon Instruments 1973, 1977). Exchangeable calcium, magnesium, and potassium were also measured in the NaCl extract following Chapman's procedure (1965) with cations analyzed by atomic absorption spectrophotometry following the addition of LaCl in 50% HCL.

Two additional subsamples of each soil sample were incubated in covered cups at air temperature in the dark for 10 days. Nitrate-N and ammonium-N were then extracted and analyzed as above. Potential net nitrogen mineralization was calculated as final $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$ minus initial $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$. Net nitrification was estimated as final minus initial $\text{NO}_3\text{-N}$.

Two 50 g subsamples were used to estimate microbial biomass N using a modification of Jenkinson and Powlson's (1976) chloroform fumigation procedure. One mL chloroform was poured over each sample, aired after 24 h, incubated for 10 days, extracted as described above and analyzed for $\text{NH}_4\text{-N}$. Microbial biomass N was calculated as the amount of nitrogen released upon fumigation, divided by a recovery coefficient (Voroney and Paul 1984) which we assumed to be 0.33 (Vitousek and Matson 1988).

Exchangeable $\text{P}_{0.4}\text{-P}$ was measured in two additional subsamples after extraction in $\text{NH}_4\text{F-HCL}$ followed by colorimetric analysis (Technicon Instruments 1977). Finally, pH in two subsamples was measured in a 2:1 slurry of CaCl_2 to fresh soil.

Moisture content of fresh soil was calculated after drying at 100°C for 48 hr. Dried subsamples were returned to ARC, ground with a rock grinder, and analyzed for total N, P, and C. Total N and P were measured using a continuous flow analyzer following block digestion with a sulfuric acid-mercuric oxide catalyst (Scientific Instruments 1981). Organic matter content of the soil was estimated by loss on ignition at 500°C for 4 hr. To develop a relationship between organic matter and total carbon content, ten subsamples were analyzed for carbon content using a Perkin Elmer Model 240B Elemental Analyzer. Carbon concentrations in all samples were estimated using the regression equation relating carbon (C) to loss on ignition organic matter (OM): $C = 0.453 \times \text{OM} + 0.174$ ($r = 0.966$).

Plant nutrients and photosynthesis

In April 1986 and March 1987, measurements of foliar N and P, specific leaf area, and photosynthesis and stomatal conductance were carried out. At each date, five individuals of each species were selected and measurements carried out on two fully expanded leaves of each individual. Photosynthesis and stomatal conductance were measured on attached leaves in the field using a LI-6000 portable photosynthesis system (LI-COR 1983) with a 0.25 L leaf chamber. All measurements took place when photosynthetically active radiation (PAR) levels were above $1400 \mu\text{mol m}^{-2}\text{s}^{-1}$. Laboratory meas-

urements of photosynthetic rates in *Myrica*, *Metrosideros*, and *Buddleja* under varying light levels indicated that photosynthesis was light saturated above $600 \mu\text{mol m}^{-2}\text{s}^{-1}$.

After measurement, leaves were removed and trimmed to the area held within the chamber, and fresh leaf area was measured using an image analysis system. Leaves were then dried at 60°C for 48 hr, weighed, returned to ARC, ground, and analyzed for total N and P as described above. Starch concentrations were measured in leaves from three individuals of each species, following the method of Matson and Waring (1984). Specific leaf area was calculated as fresh leaf area per dry weight.

Litter nutrients and decomposition

Recently abscised leaves were also collected from under or on each shrub at the time of foliar sampling. This litter was dried, ground, and analyzed for total N, P, and C as described above. Decomposition studies were carried out on abscised leaves of *Myrica*, *Metrosideros*, and *Buddleja* using the tethered leaf method. Air dried leaves were weighed individually and their petioles were tied with fishing line into strings of five leaves. Air-dried weight was corrected to oven dried weight by drying weighed subsamples at 70°C and reweighing. The strings were placed under isolated *Myrica*, *Metrosideros*, and *Buddleja* in the site. For *Metrosideros* and *Myrica*, three strings of each were collected after 1, 3, 6, 12, 18, and 24 mo. (Vitousek and Walker 1989); for *Buddleja*, strings were collected at six time points in the first six months. After collection, leaves were oven dried and weighed; strings were considered the sampling unit.

Results

Soil characteristics

The influence of vegetation on soil properties was clearly evident in the comparison of plant areas vs. open areas (Table 1). Exchangeable cations were greatly increased in areas of vegetation cover, as were soil carbon and nitrogen. Total phosphorus concentrations, on the other hand, did not differ significantly between open and most plant covered areas. In newly deposited volcanic substrates such as these, phosphorus levels and availability are presumably already very high in relation to other nutrients (Walker and Syers 1976).

Table 1. Soil properties under isolated individuals of woody plants. Values are means of 10 individuals sampled to 15 cm depth, with standard errors in parenthesis

	Total C %	Total N %	Total P %	pH	Ca $\mu\text{g/g}$	Mg	K
Native Species							
<i>Metrosideros</i>	2.99 (0.45)	0.11 (0.02)	0.023 (0.001)	5.08 (0.13)	422 (55)	71 (9)	23 (5)
<i>Vaccinium</i>	1.19 (0.15)	0.05 (0.01)	0.019 (0.001)	5.95 (0.11)	123 (14)	39 (5)	24 (2)
<i>Dubautia</i>	1.18 (0.27)	0.05 (0.02)	0.014 (0.002)	5.85 (0.08)	239 (63)	35 (9)	25 (6)
Exotic Species							
<i>Myrica</i>	2.45 (0.27)	0.10 (0.01)	0.009 (0.002)	5.47 (0.08)	186 (19)	72 (6)	13 (3)
<i>Buddleja</i>	2.87 (0.43)	0.15 (0.02)	0.031 (0.003)	5.60 (0.08)	213 (32)	73 (10)	33 (5)
Bare Ground							
Open	0.65 (0.11)	0.02 (0.01)	0.019 (0.002)	5.20 (0.05)	2 (1)	5 (1)	1 (1)

Table 2. Nitrogen pools, nitrogen mineralization, nitrification, microbial biomass nitrogen, and extractable PO₄-P in soils. Values are means (\pm standard error) of ten individuals per species

	NH ₄ -N μg/g	NO ₃ -N μg/g	Mineralization μg·g ⁻¹ ·10 d ⁻¹	Nitrification μg·g ⁻¹ ·10 d ⁻¹	Microbial Biomass N μg/g	PO ₄ -P μg/g
Native species						
<i>Metrosideros</i>	0.9 (0.4)	0.5 (0.2)	0.5 (0.5)	0.3 (0.3)	20.7 (2.0)	6.1 (0.7)
<i>Vaccinium</i>	0.4 (0.2)	0.2 (0.1)	-0.4 (0.2)	-0.1 (0.1)	7.5 (1.2)	9.4 (0.7)
<i>Dubautia</i>	0.3 (0.1)	0.1 (0.1)	0.4 (0.3)	0.2 (0.2)	16.0 (3.2)	8.3 (0.7)
Exotic species						
<i>Myrica</i>	2.7 (1.1)	3.7 (0.9)	3.5 (1.1)	4.9 (1.6)	35.8 (6.0)	8.7 (0.8)
<i>Buddleja</i>	1.5 (0.4)	2.1 (0.4)	2.2 (0.6)	2.1 (0.4)	37.9 (8.9)	12.7 (0.5)
Bare Ground						
Open	0.4 (0.2)	0.2 (0.05)	-0.2 (0.1)	0.05 (0.07)	1.3 (0.8)	7.4 (0.7)

Table 3. Foliar characteristics of 5 species. Values are means (\pm standard errors). Superscripts show the n of the mean (the number of individuals sampled). Each individual had 2–3 leaves sampled

	Foliar N %	Foliar P %	Foliar Starch %	Specific Leaf weight g/m ²	Photosynthesis nmol · g ⁻¹ · sec ⁻¹
Native Species					
<i>Metrosideros</i>	0.88 (0.041) ¹²	0.074 (0.006) ¹²	0.63 (0.020) ³	218.2 (9.9) ¹²	38.05 (2.24) ¹²
<i>Vaccinium</i>	0.81 (0.057) ¹¹	0.063 (0.002) ¹¹	0.47 (0.066) ³	143.9 (3.0) ¹¹	30.95 (3.18) ¹¹
<i>Dubautia</i>	1.39 (0.062) ¹⁰	0.156 (0.007) ¹⁰	0.59 (0.018) ³	108.7 (5.6) ¹⁰	75.56 (6.28) ¹⁰
Exotic Species					
<i>Myrica</i>	1.34 (0.059) ¹¹	0.052 (0.004) ¹¹	0.99 (0.22) ³	131.9 (5.2) ¹¹	57.32 (5.85) ¹¹
<i>Buddleja</i>	2.50 (0.140) ¹¹	0.206 (0.015) ¹¹	2.38 (0.33) ³	68.0 (6.8) ¹¹	166.96 (13.38) ¹¹

Some clear differences in soil characteristics also were evident among species (Table 1). In terms of total carbon and nitrogen concentrations in the soil, the native *Metrosideros* functioned similarly to the two exotics, accumulating two-fold greater concentrations than *Vaccinium* and *Dubautia*. The same pattern followed for Mg, but not for the other cations. Phosphorus concentrations, in contrast, ranged from 0.009 to 0.031%, with soil under the exotic *Myrica* the lowest and under the exotic *Buddleja* the highest. A similar pattern was found for potassium (Table 1).

In a comparison of soil inorganic nitrogen concentrations and nitrogen cycling processes, major and consistent differences were found between the native and exotic species. Both exotic species clearly had much greater inorganic and microbial concentrations of nitrogen, and faster soil turnover of nitrogen, than did the native species (Table 2). The native species had, in many cases, N concentrations and rates of N turnover not different from open soil. As with total phosphorus, extractable P did not differ strikingly between most plant-influenced areas and open soil; it was, however, significantly elevated under *Buddleja*.

Plant nutrients and processes

Foliar concentrations of nitrogen were markedly higher in the exotics than in *Metrosideros* or *Vaccinium* (Table

3). Surprisingly, *Buddleja*, a non-fixer, had higher N levels than did the N-fixer *Myrica* (t-test, $p < 0.001$). *Buddleja* also had significantly higher P concentrations and starch concentrations than all other species (t-test, $p > 0.05$). Because leaf weight per area was lower in *Buddleja*, however, area-based leaf nitrogen in *Myrica* and *Buddleja* were similar. *Dubautia*, a non N-fixing native species, had N concentrations as high as *Myrica*, but on an areal basis, *Dubautia*'s foliar N was lower than all other species (Table 3). Across all species, leaf weight per area varied inversely with nitrogen concentration (Fig. 1). The sclerophyllous *Metrosideros* had the greatest weight per area and lowest weight-based nitrogen concentrations; *Buddleja*, with thin fragile leaves, had specific leaf weights similar to many annuals (Field and Money 1986), and very high nitrogen concentrations.

Leaf net photosynthesis varied among species. *Buddleja* had the highest rates, *Myrica* and the native *Dubautia* were intermediate, and *Vaccinium* and *Metrosideros* were lowest (Table 3). Photosynthesis was strongly and linearly related to leaf nitrogen on a weight basis (Fig. 2; $r = 0.83$ $p < 0.001$). This linearity across species has been reported earlier (for example, Field and Mooney 1986). Within species, a clear positive relationship was not evident. Across all species stomatal conductance was also linearly related to net photosynthesis (Fig. 3).

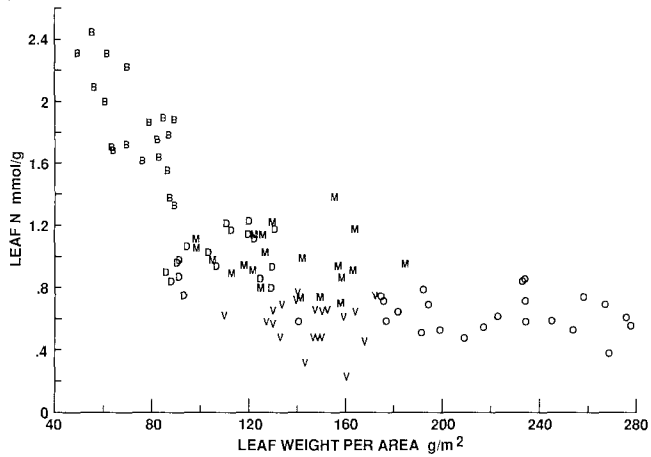


Fig. 1. Leaf weight per area (g/m^2) vs. foliar nitrogen (mmol/g) for individual leaves across all species; B, *Buddeleja*; D, *Dubautia*; M, *Myrica*; V, *Vaccinium*; O, *Metrosideros* (common name Ohia)

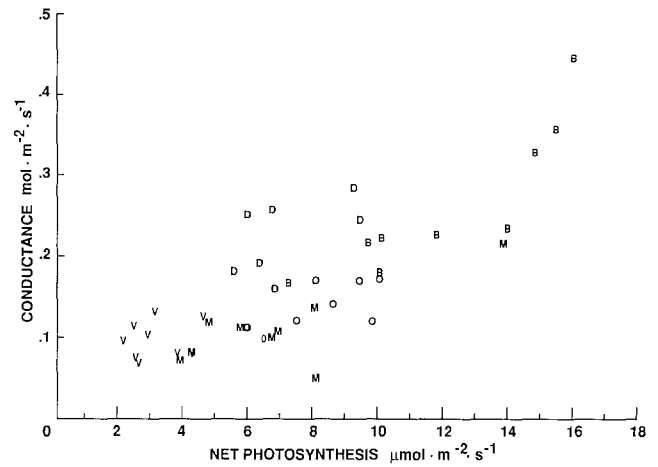


Fig. 3. Net photosynthesis ($\text{nmol m}^{-2}\text{s}^{-1}$) vs. foliar conductance ($\text{mol m}^{-2}\text{s}^{-1}$) for individual leaves across all species measured in 1987. Symbols are as in Fig. 1

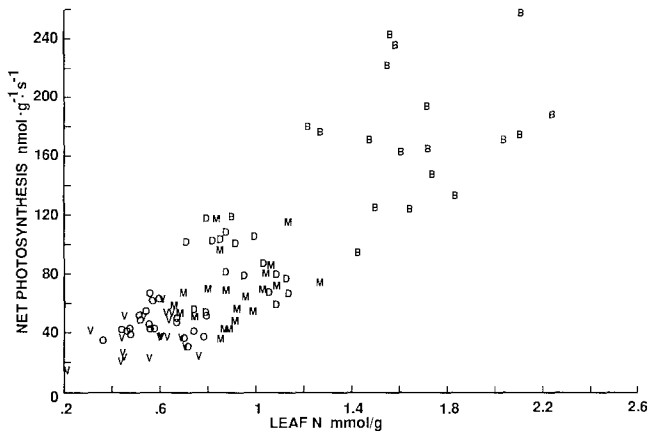


Fig. 2. Leaf nitrogen (mmol/g) vs. net photosynthesis ($\text{nmol g}^{-1}\text{s}^{-1}$) for individual leaves across all species. Symbols as in Fig. 1

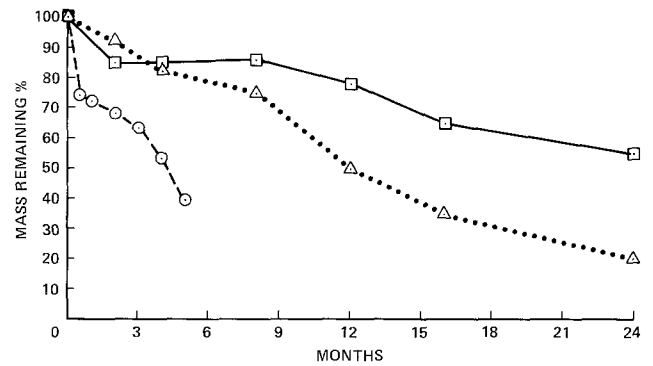


Fig. 4. Decomposition (represented as percent of original mass remaining over time) for *Metrosideros* (—□—), *Myrica* (...△...) and *Buddeleja* (—○—)

Table 4. Concentrations of total N, P and C in abscised leaves. Values are means (\pm standard errors) of 10 individuals

	N %	P %	C %	C:N
Native Species				
<i>Metrosideros</i>	0.69 (0.05)	0.07 (0.002)	39.64 (1.2)	57
<i>Vaccinium</i>	0.62 (0.07)	0.07 (0.004)	30.28 (2.4)	48
<i>Dubautia</i>	0.60 (0.05)	0.05 (0.003)	37.18 (0.65)	64
Exotic Species				
<i>Myrica</i>	1.32 (0.07)	0.006 (0.002)	38.3 (1.34)	27
<i>Buddeleja</i>	1.59 (0.14)	0.12 (0.009)	35.8 (2.48)	22

Litter nutrients and decomposition

The chemistry of senesced leaves of the five shrubs differed substantially (Table 4); the natives had low concentrations of nitrogen (0.60–0.69%) and phosphorus (0.05–0.07%) commensurate with their low foliar concentrations (Table 3). *Myrica* leaf litter, on the other

hand, had high nitrogen concentrations (averaging 1.32%) and very low phosphorus concentrations (0.006%), indicating greater retranslocation of phosphorus than of nitrogen. *Buddeleja* leaf litter nitrogen and phosphorus concentrations were 1.59% and 0.12% respectively (Table 4); apparent retranslocation of nitrogen based on leaf concentrations was greater than that

of all other species except *Dubautia*; apparent phosphorus retranslocation was less than in *Myrica* and *Dubautia*, but greater than the other native species.

Rates of decomposition in *Myrica*, *Buddleja*, and *Metrosideros* reflected their initial nitrogen levels and C:N ratios. *Buddleja*'s senesced leaves lost 60% of original mass within six months (Fig. 3). *Myrica* leaves lost 60% after 16 months, but *Metrosideros* lost only about 35% of original mass after 24 months (Fig. 3, from Vitousek and Walker 1989).

Discussion

Plant-soil interactions

In general, the correlations between plant processes and soil characteristics in this site are strong. For the exotics *Buddleja* and to a lesser extent *Myrica*, plant concentrations of nitrogen are high, accompanied by high photosynthetic rates and high concentrations of non-structural carbon in the leaves. The leaves, which tend to be less sclerophyllous than the natives, have relatively low C:N ratios after they senesce, and they decompose relatively quickly. Soil under these shrubs is relatively rich in nitrogen, organic matter, and cations. Rates of nitrogen mineralization and nitrification, which can be used as indices of nitrogen available to the plants, are high and are reflected in high leaf nutrient levels.

At the other extreme, native species like *Metrosideros* and *Vaccinium* have low leaf nutrient concentrations, low net photosynthetic rates, high leaf C:N ratios and low leaf decomposition rates, and low available pools and turnover rates of N in the soil. Thus, for the low nutrient native plants as well as for the high nutrient exotics, a strong correlation exists between plant processes and soil characteristics.

Myrica is a symbiotic N-fixer, so its high nitrogen status and influence on N availability were expected. However, the high N found in and under *Buddleja* is not as easily explained. As noted earlier, *Buddleja* had very high net photosynthetic rates associated with high concentrations of foliar N, and soil N concentrations and processes were all higher than found in any other species. It appears that *Buddleja* either 1) has greater ability to acquire nutrients through higher root absorption capacity, greater root proliferation, or perhaps mycorrhizal associations; or 2) colonizes uniquely fertile microsites and can then maintain site fertility. Preliminary data suggest that *Buddleja* does have mycorrhizae, but so do other species in the area (Vitousek and Woodward, personal communications). Other preliminary data show no differences in extractable P between soil under 8 small (< 20 cm tall, single stem) *Buddleja* seedlings and composited uncolonized soil samples in the Devastation Trail area; $\text{NH}_4\text{-N}$ concentrations, on the other hand, were higher under the seedlings than in the open soil ($1.15 \pm 0.25 \mu\text{g/g}$ vs. $0.35 \mu\text{g/g}$ respectively). These data support the possibility that *Buddleja* colonizes rich mi-

crosites. In addition, Mueller-Dombois and Whiteaker (in press) reported that vegetation analysis of the same area suggests that *Buddleja* is frequently associated with dead standing *Metrosideros* stems, presumably because of improved soil microenvironment.

Implications for further colonization

If plants are capable of altering soil nutrient availability beneath them, there is a potential for that alteration to affect the further colonization of a site. Mueller-Dombois and Whiteaker (in press) examined associations of weed species with individuals of *Buddleja*, *Myrica*, and *Metrosideros* in the Devastation Trail area. They concluded that *Buddleja* clearly facilitates invading species. On the other hand, there was no preferential association of weed species with *Myrica*. Despite the improved soil nitrogen and organic matter status under *Myrica*, it apparently does not encourage the growth of other invading species in this site. The low light levels ($< 15 \mu\text{mol m}^{-2}\text{s}^{-1}$ in contrast to $> 70 \mu\text{mol m}^{-2}\text{s}^{-1}$ under *Buddleja*; Vitousek personal communication) found under its very dense canopies may contribute to this result, as may the extremely low soil phosphorus concentrations beneath the canopy.

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