

Suffix Trees

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Algorithms on Strings
Data Structures and Algorithms

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([Algorithms and Data Structures](#) Specialization)

Outline

- **From Genome Sequencing to Pattern Matching**
- Brute Force Approach to Pattern Matching
- Herding Patterns into Trie
- Herding Text into Suffix Trie
- From Suffix Tries to Suffix Trees

The Newspaper Problem



stack of NY Times, June 27, 2000

The Newspaper Problem



stack of NY Times, June 27, 2000



stack of NY Times, June 27, 2000
on a pile of dynamite

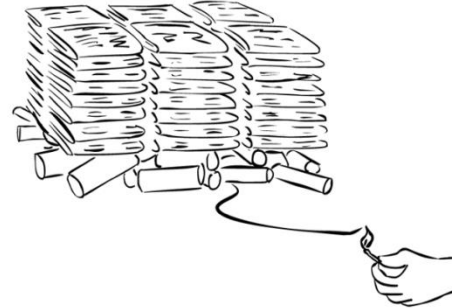
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this is just hypothetical

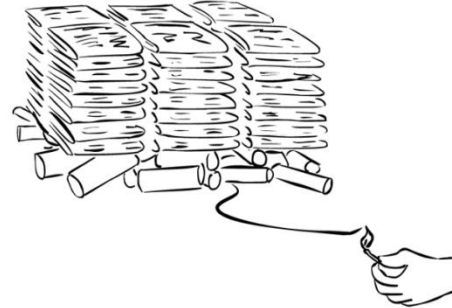
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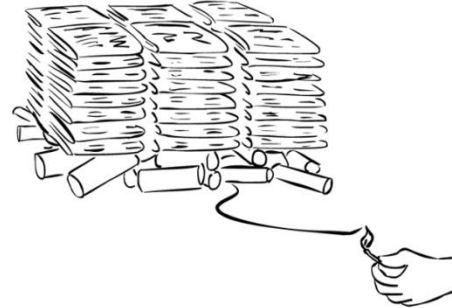
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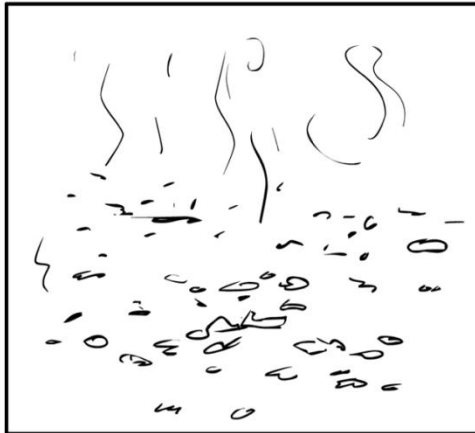
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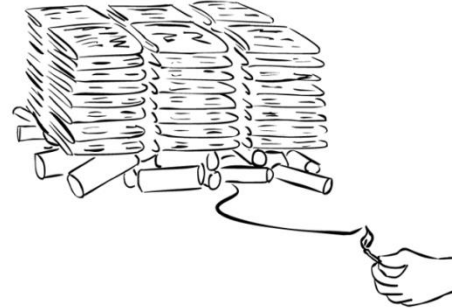
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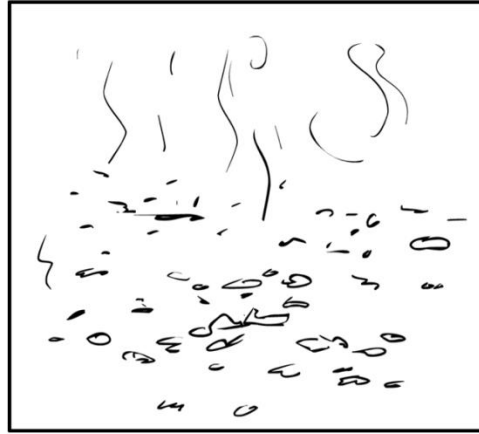


this is just hypothetical



so, what did the June 27, 2000 NY
Times say?

The Newspaper Problem as an Overlapping Puzzle



...noodie, appr
...e have not yet named
...mation is welc

...lie, appr
...yet named any suspects, alt
...is welc
...e ca

The Newspaper Problem as an Overlapping Puzzle



...noodie, appr
...e have not yet named
...mation is welc

...die, appr
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...is welc
...e ca

Millions of Copies of a Genome



CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTACCACATCGTAGCTACGATGCATTAGCAAGCTATCGGATCAGCTACCACATCGTAGC
CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTACCACATCGTAGCTACGATGCATTAGCAAGCTATCGGATCAGCTACCACATCGTAGC
CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTACCACATCGTAGCTACGATGCATTAGCAAGCTATCGGATCAGCTACCACATCGTAGC
CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTACCACATCGTAGCTACGATGCATTAGCAAGCTATCGGATCAGCTACCACATCGTAGC

Breaking the Genomes at Random Positions



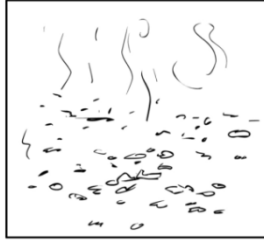
CTGATGATGGACTACGCTACTACTGCTGCTGTATTATGATCAGCTACCATCGTAGCTATGATGCATTAGCATCTATCGCTCAGCTACCATCGTAGC
CTGATGATGGACTACGCTACTACTCTAGCTGTATACGATCAGCTACCATCGTAGCTACGATGCATTAGCAAGCTTCGGATCATACCATCATCTAGC
CTGATGATGGACTACGCTACTACTGCTATCTGTATTATGATCAGCTACCATCGTAGCTACGATGCATTAGCAAGCTATGGATCAGCTACCATCGTAGC
CTGATGATGCTACGCTACTGCTAGCTTATTACGATGCTACCACATCGTAGCTACGATGCATTAGCATCTATCGGATCAGCTACCATCTAGC

Generating Short Substring (Reads)



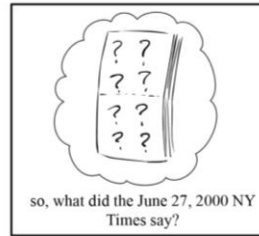
CTGATGA TGGACTACGCTAC TACTGCTAG CTGTATTACG ATCAGCTACCACA TCGTAGCTACG ATGCATTAGCAA GCTATCGGA TCAGCTACCA CATCGTAGC
CTGATGATG GACTACGCT ACTACTGCTA GCTGTATTACG ATCAGCTACC ACATCGTAGCT ACGATGCATTA GCAAGCTATC GGATCAGCTAC CACATCGTAGC
CTGATGATGG ACTACGCTAC TACTGCTAGCT GTATTACGATC AGCTACCAC ATCGTAGCTACG ATGCATTAGCA AGCTATCGG A TCAGCTACCA CATCGTAGC
CTGATGATGGACT ACGCTACTACT GCTAGCTGTAT TACGATCAGC TACCACATCGT AGCTACGATGCA TTAGCAAGCT ATCGGATCA GCTACCACATC GTAGC

Burning Some Reads



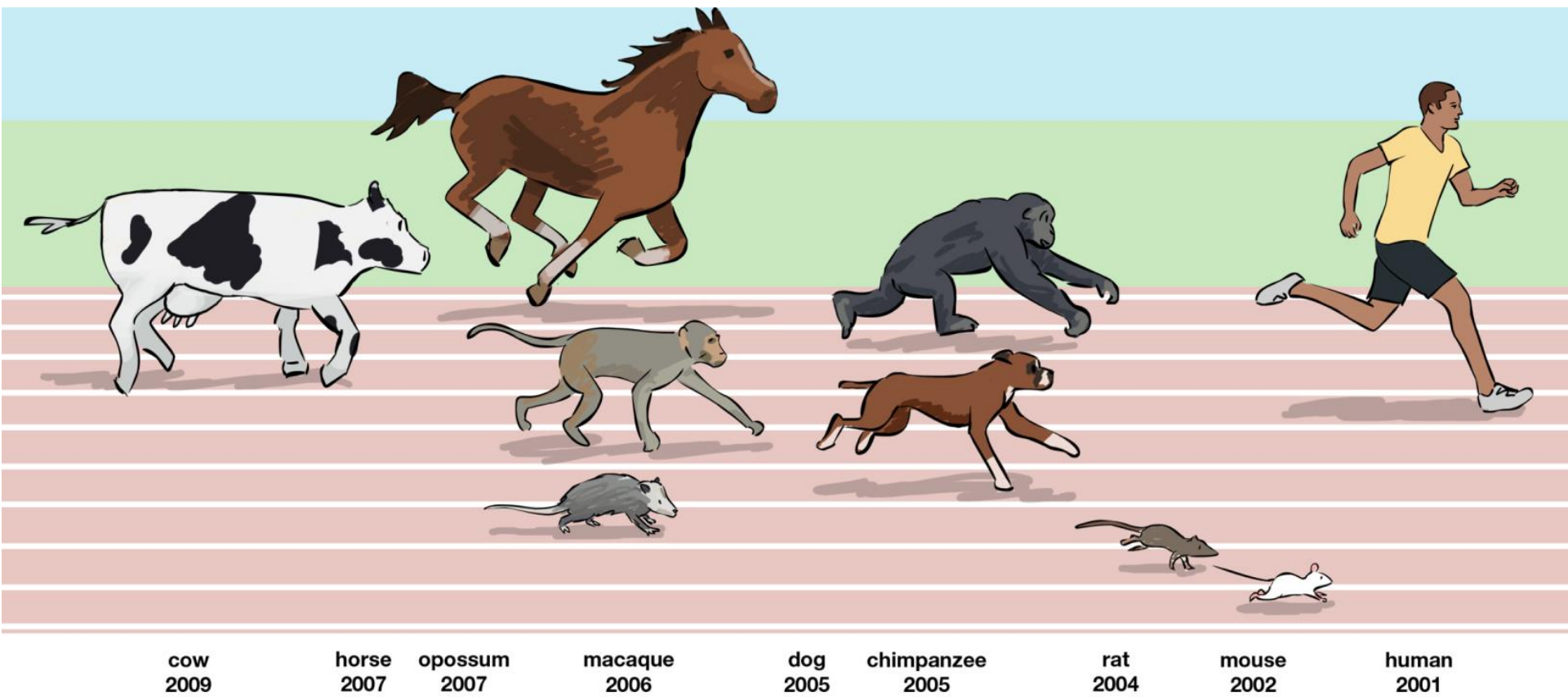
CTGATGA TGGACTACGCTAC TACTGCTAG CTGTATTACG ATCAGCTACCACA TCGTAGCTACG ATGCATTAGCAA GCTATCGGA TCAGCTACCA CATCGTAGC
CTGATGATG GACTACGCT ACTACTGCTA GCTGTATTACG ATCAGCTACC ACATCGTAGCT ACGATGCATTA GCAAGCTATC GGATCAGCTAC CACATCGTAGC
CTGATGATGG ACTACGCTAC TACTGCTAGCT GTATTACGATC AGCTACCAC ATCGTAGCTACG ATGCATTAGCA AGCTATCGG A TCAGCTACCA CATCGTAGC
CTGATGATGGACT ACGCTACTACT GCTAGCTGTAT TACGATCAGC TACCACATCGT AGCTACGATGCA TTAGCAAGCT ATCGGATCA GCTACCACATC GTAGC

Assembling Genome



CTGATGA TGGACTACGCTAC TACTGCTAG CTGTATTACG ATCAGCTACCACA TCGTAGCTACG ATGCATTAGCAA GCTATCGGA TCAGCTACCA CATCGTAGC
CTGATGATG GACTACGCT ACTACTGCTA GCTGTATTACG ATCAGCTACC ACATCGTAGCT ACGATGCATTA GCAAGCTATC GGATCAGCTAC CACATCGTAGC
CTGATGATGG ACTACGCTAC TACTGCTAGCT GTATTACGATC AGTACCAC ATCGTAGCTACG ATGCATTAGCA AGTATATCGG A TCAGCTACCA CATCGTAGC
CTGATGATGGACT ACGCTACTACT GCTAGCTGTAT TACGATCAGC TACCACATCGT AGCTACGATGCA TTAGCAAGCT ATCGGATCA GCTACCACATC GTAGC





Why Do We Sequence 1000s of Species?



Applications in

- **medicine** (mouse genome)
- **agriculture** (rice genome)
- **biotechnology** (genomes of energy-producing bacteria),
- etc., etc., etc.

Few Mutations Can Make a Big Difference...

- Different people have slightly different genomes:
on average, roughly 1 mutation in 1000 nucleotides.
- The 1 in 1000 nucleotides difference accounts for height,
high cholesterol susceptibility, and 7000+ genetic diseases.

```
CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGA  
TCAGCTACCACATCGTAGCTACGATGCATTAGCAAGCTAT  
CGATCGATCGATCGATTATCTACGATCGATCGATCGATCA  
CTATACGAGCTACTACGTACGTACGATCGCGGGACTATTA  
TCGACTACAGATAAAACATGCTAGTACAACAGTATACATA  
GCTGCGGGATACGATTAGCTAATAGCTGACGATATCCGAT
```

```
CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGA  
TCAGCTACAACATCGTAGCTACGATGCATTAGCAAGCTAT  
CGATCGATCGATCGATTATCTACGATCGATCGATCGATCA  
CTATACGAGCTACTACGTACGTACGATCGCGTGACTATTA  
TCGACTACAGATGAAACATGCTAGTACAACAGTATACATA  
GCTGCGGGATACGATTAGCTAATAGCTGACGATATCCGAT
```

Emergence of Personalized Medicine

- **2010:** Nicholas Volker became the first child to be saved by genome sequencing.
 - Doctors could not diagnose his condition; he went through dozens of surgeries.
 - Sequencing revealed a mutation in a gene linked to a defect in his immune system.
 - This led doctors to use immunotherapy, which saved the child.

From Reference Genome to Personal Genomes

- **Reference human genome** assembled in 2000.

CTGAGGATGGACTACGCTACTACTGATAGCTGTTT reference
genome

GAGGA C**C**ACG TGA-AG
CTGA GGAC**C** ACTAC A-AGCT reads
 GATGG ACGCT TGTTT

CTGAGGATGGAC**C**ACGCTACTACTGA-AGCTGTTT personal
genome



Exact Pattern Matching

- Where does a read match the reference genome *exactly*?
- **Pattern Matching Problem:**
 - **Input:** A string *Pattern* (read) and a string *Text* (genome).
 - **Output:** All positions in *Text* where *Pattern* appears as a substring.

Approximate Pattern Matching

- Where does a read match the reference genome *approximately*?
- **Approximate Pattern Matching Problem:**
 - **Input:** A string *Pattern*, a string *Text*, and an integer d
 - **Output:** All positions in *Text* where *Pattern* appears as a substring *with at most d mismatches*.

Multiple Pattern Matching

- Where do **billions** of reads match the reference genome?
- **Multiple Pattern Matching Problem:**
 - **Input:** A **set of strings** *Patterns* and a string *Text*.
 - **Output:** All positions in *Text* where a string from *Patterns* appears as a substring.

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A Brute Force Approach to Exact Pattern Matching

Genome

CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTAC**C**ACATCGTAGCTAC



Pattern drives along *Text*

p a n a m a b a n a n a s

Text

n a n a

Pattern



p a n a m a b a n a n a s

Text

n a n a

Pattern



p a n a m a b a n a n a s

Text

n a n a

Pattern



p a **n** a m a b a n a n a s

Text

n a n a

Pattern



p a **n a** m a b a n a n a s

Text

n a n a

Pattern



p a n a m a b a n a n a s

Text

n a n a

Pattern



p a n **a** m a b a n a n a s

Text

n a n a

Pattern



p a n a **m** a b a n a n a s

Text

n a n a

Pattern



p a n a m **a** b a n a n a s

Text

n a n a

Pattern



p a n a m a **b** a n a n a s

Text

n a n a

Pattern



p a n a m a b **a** n a n a s

Text

n a n a

Pattern



p a n a m a b a **n** a n a s

Text

n a n a

Pattern



p a n a m a b a **n a** n a s

Text

n a n a

Pattern



p a n a m a b a **n a n** a s

Text

n a n a

Pattern



Pattern Found!

p a n a m a b a **n a n a** s

Text

n a n a

Pattern

.



p a n a m a b a n **a** n a s

Text

n a n a

Pattern



Brute Force Approach Is Fast!

- **single *Pattern*:** $O(|Text| \cdot |Pattern|)$



The runtime of the **Knuth-Morris-Pratt** algorithm: $O(|Text|)$
(wait for the lecture on algorithmic challenges in pattern matching)



Brute Force Approach is Slow for **Billions** of Patterns

- **single** *Pattern*: $O(|Text| \cdot |Pattern|)$
- **multiple** *Patterns*:

$$O\left(\sum_{\substack{\text{all strings } Pattern \\ \text{In } Patterns}} |Text| \cdot |Pattern|\right)$$

Brute Force Approach is Slow for Billions of Patterns

- **single *Pattern*:** $O(|Text| \cdot |Pattern|)$
- **multiple *Patterns*:**

$$O\left(\sum_{\substack{\text{all strings } Pattern \\ \text{In } Patterns}} |Text| \cdot |Pattern|\right) =$$

$$O(|Text| \cdot |Patterns|)$$

For human genome:

- $|Text| \approx 3 \cdot 10^9$
- $|Patterns| \approx 10^{12}$



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Patterns Travel One at a Time

Genome

CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTAC**C**ACATCGTAGCTAC

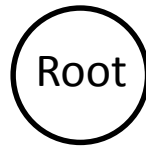


Herding Patterns onto a Bus

Genome

CTGATGATGGACTACGCTACTACTGCTAGCTGTATTACGATCAGCTACC**C**ACATCGTAGCTAC





Patterns

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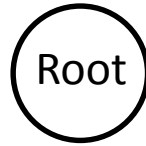
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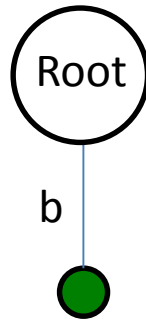
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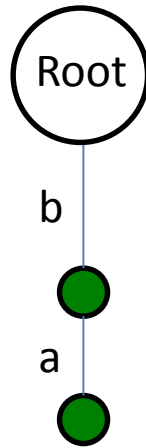
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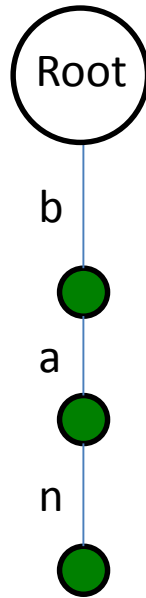
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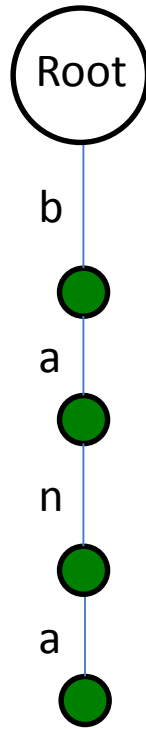
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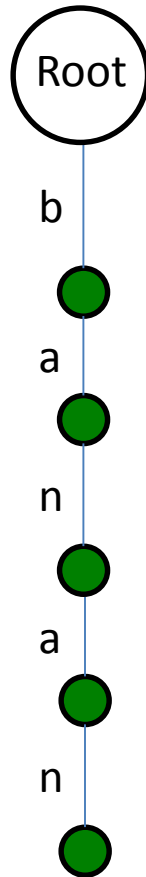
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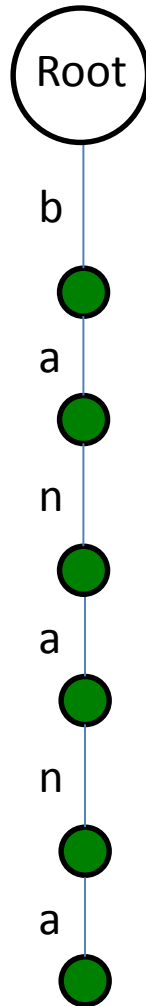
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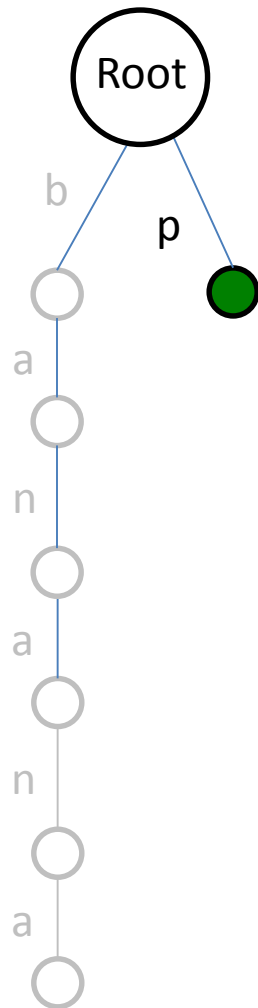
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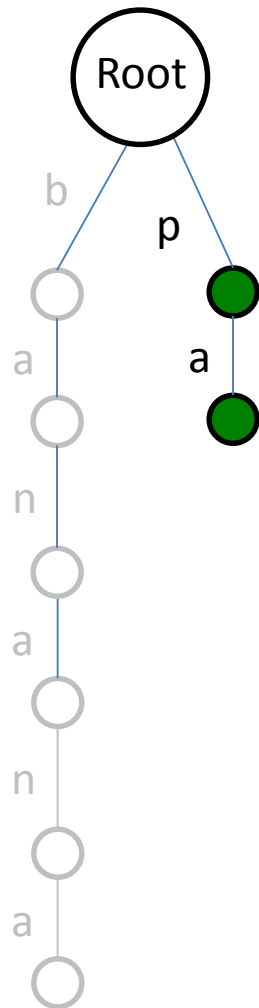
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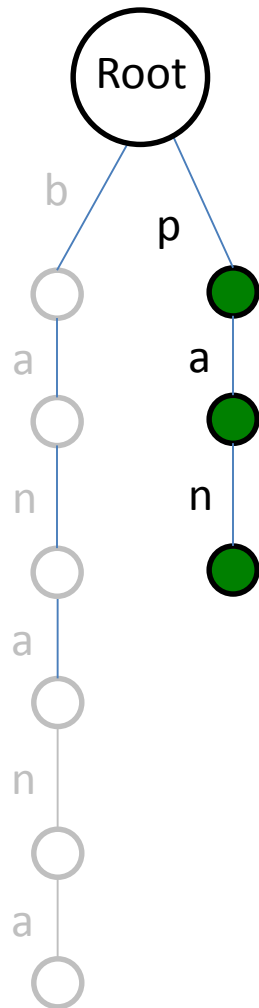
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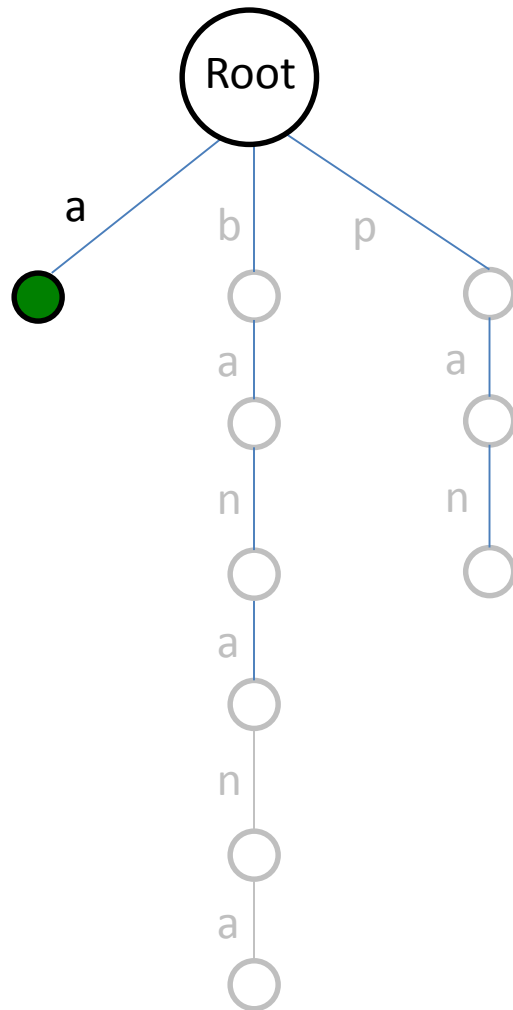
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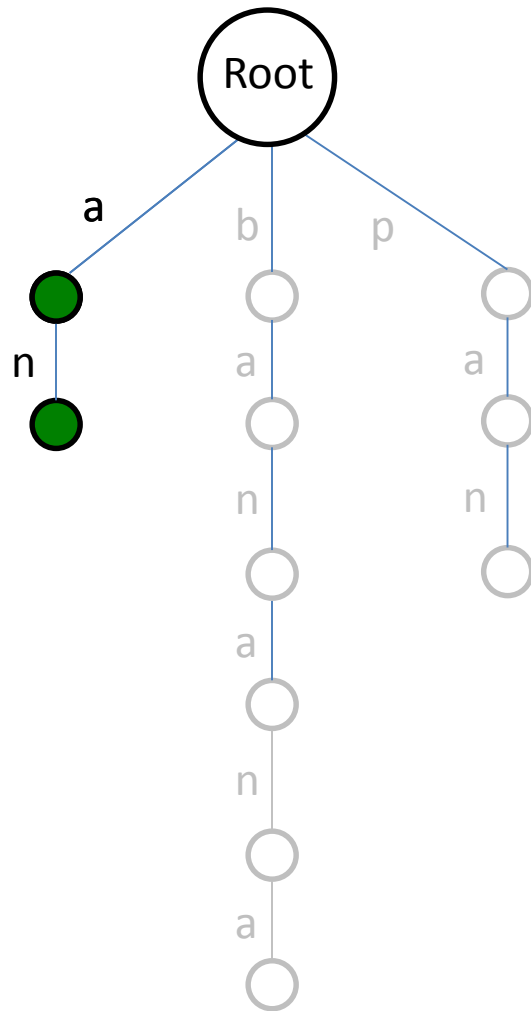
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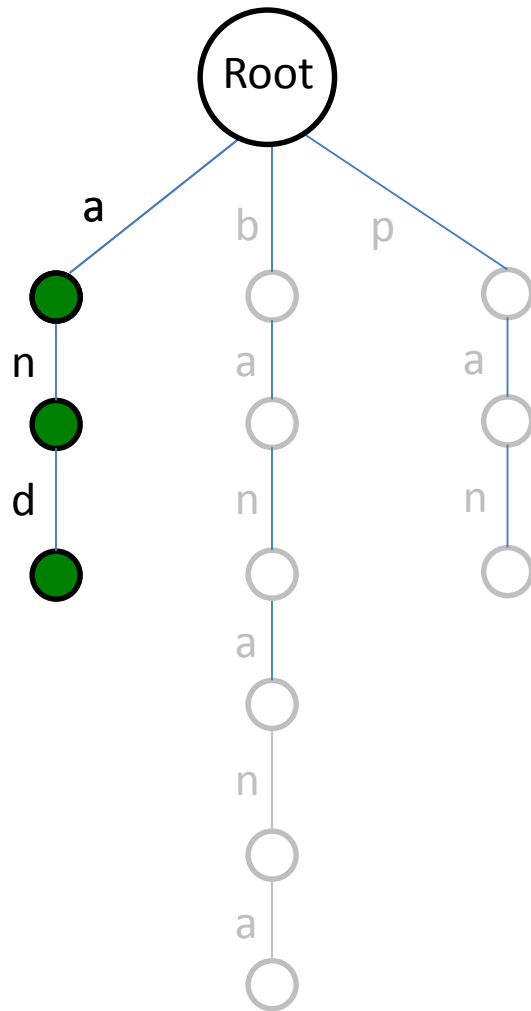
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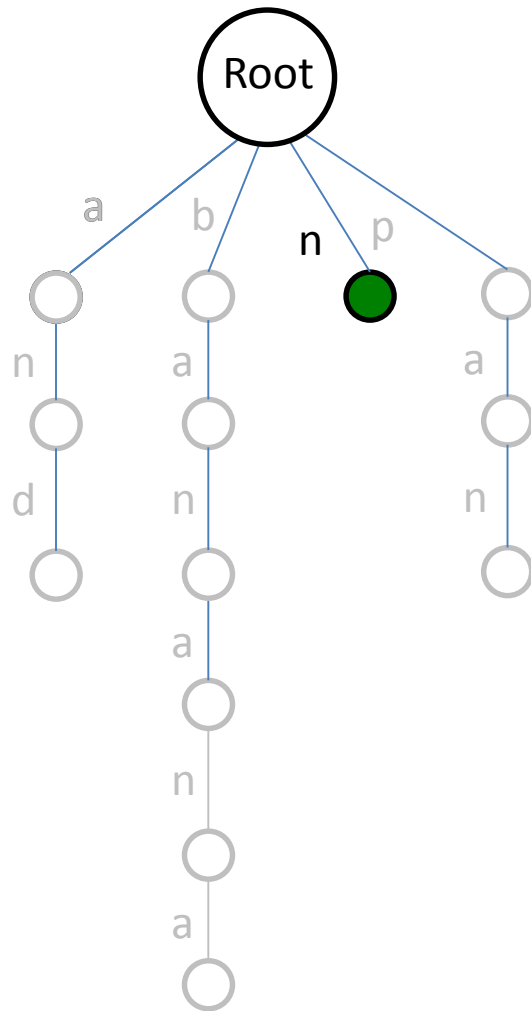
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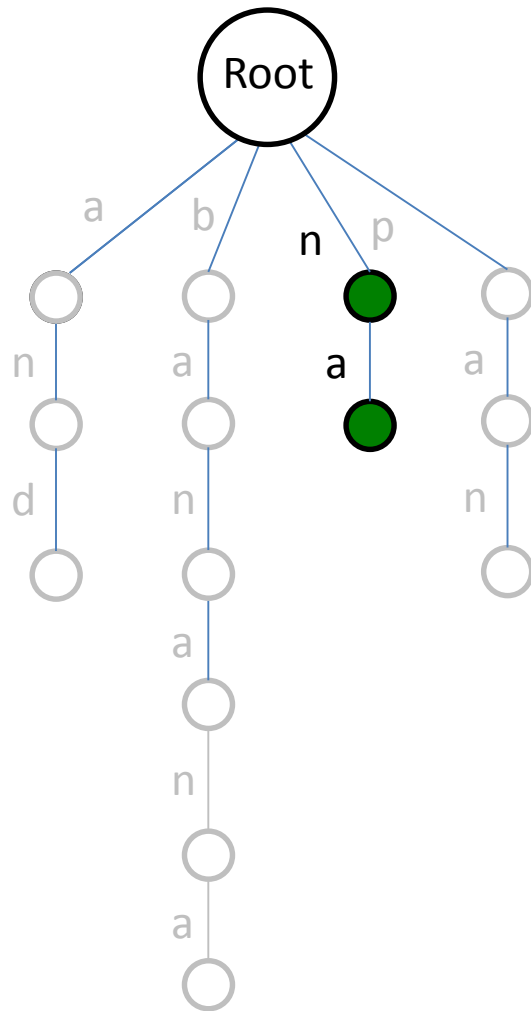
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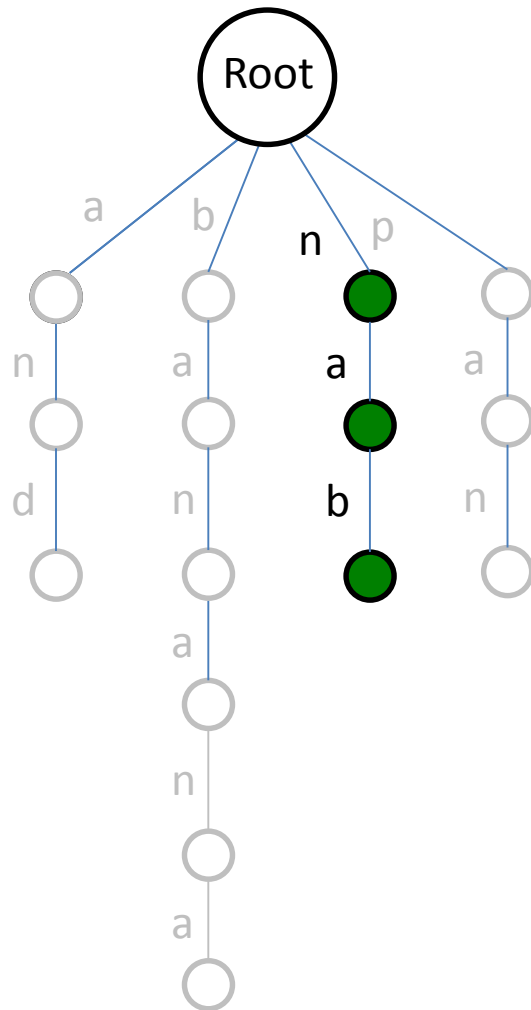
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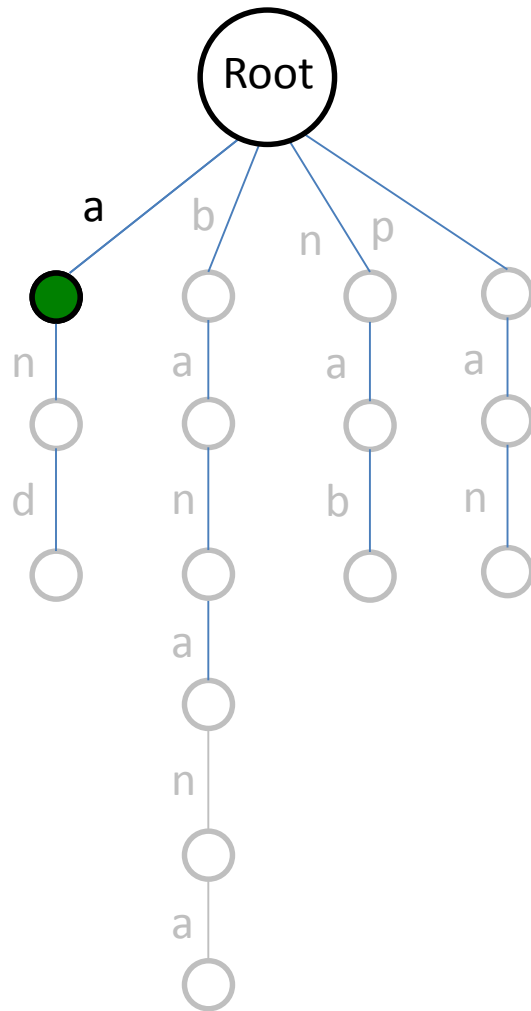
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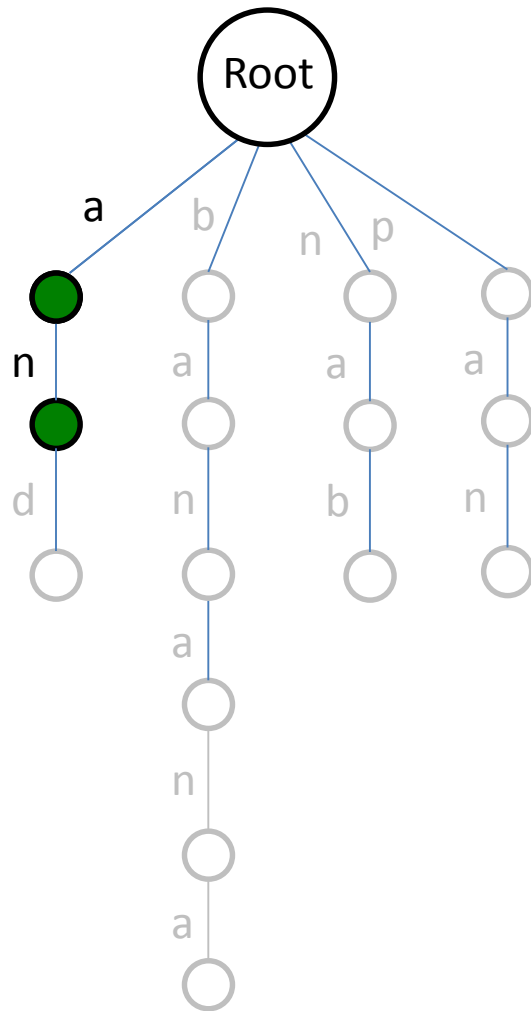
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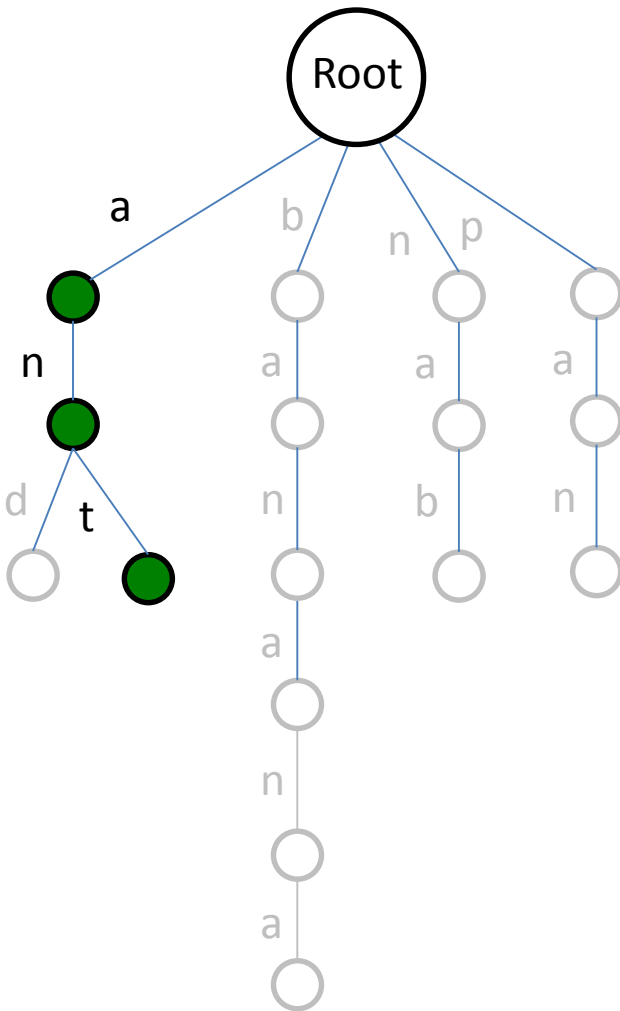
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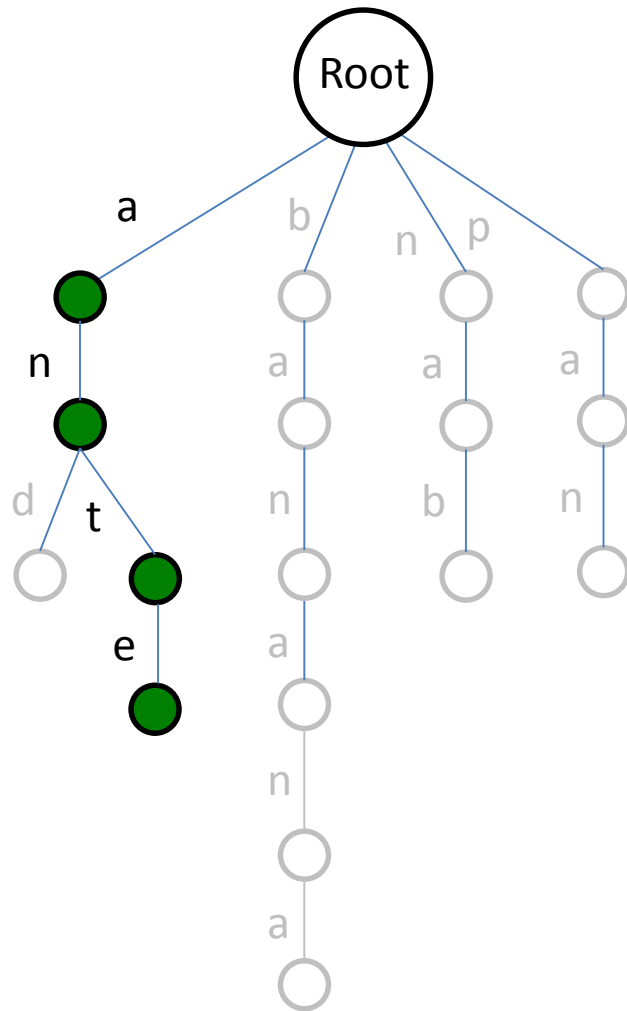
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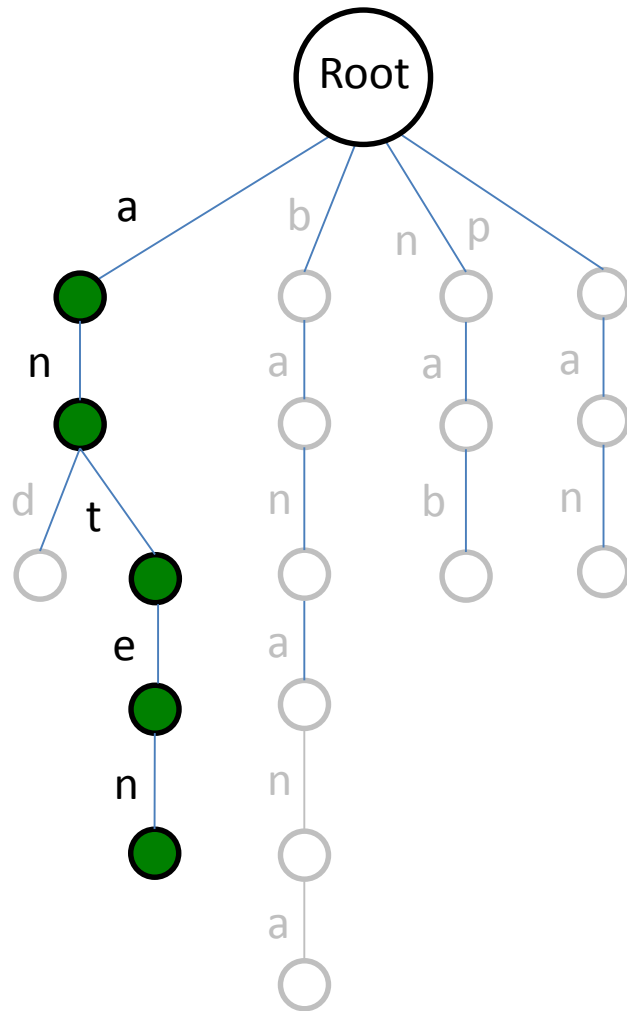
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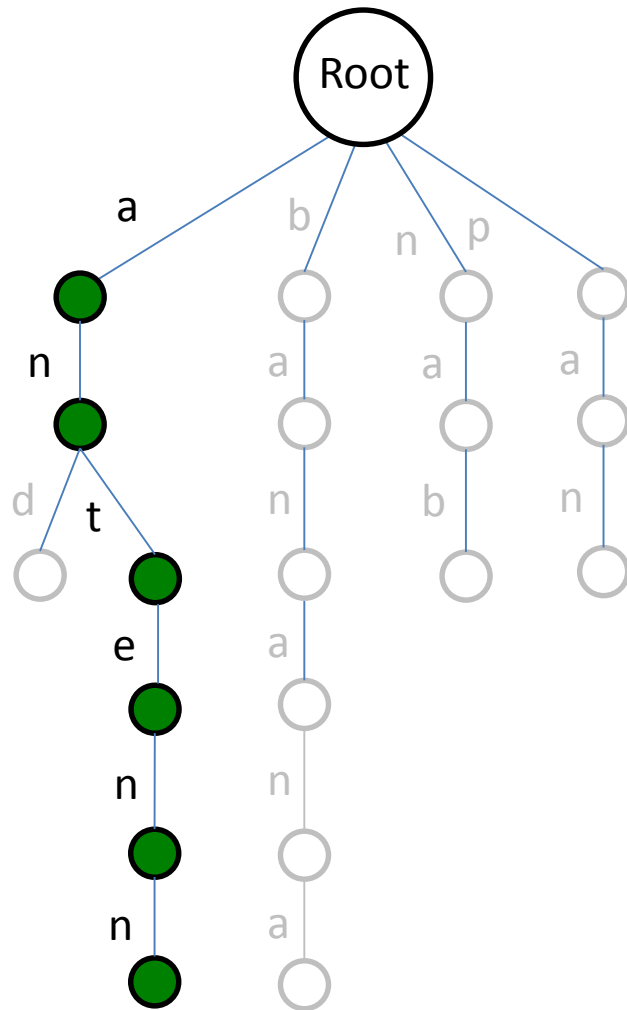
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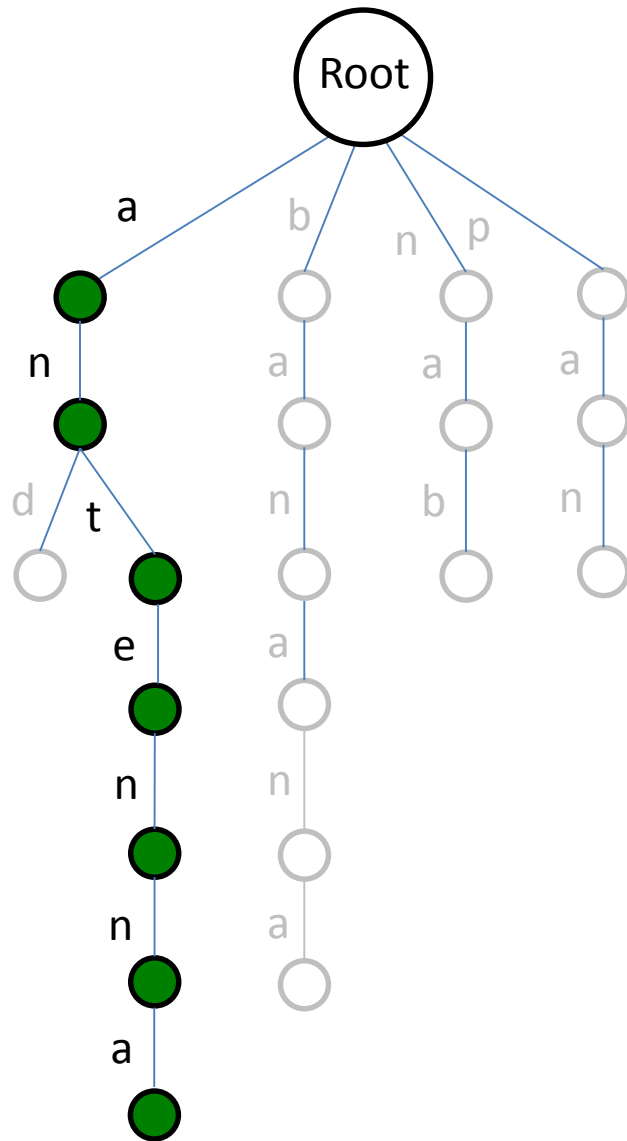
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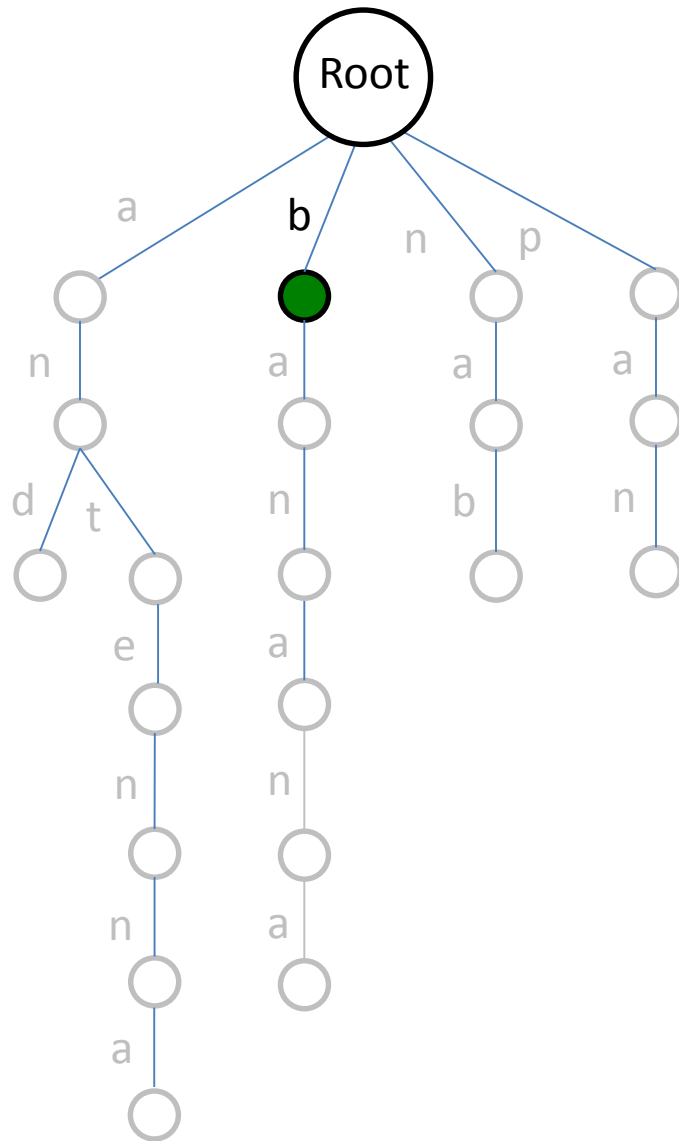
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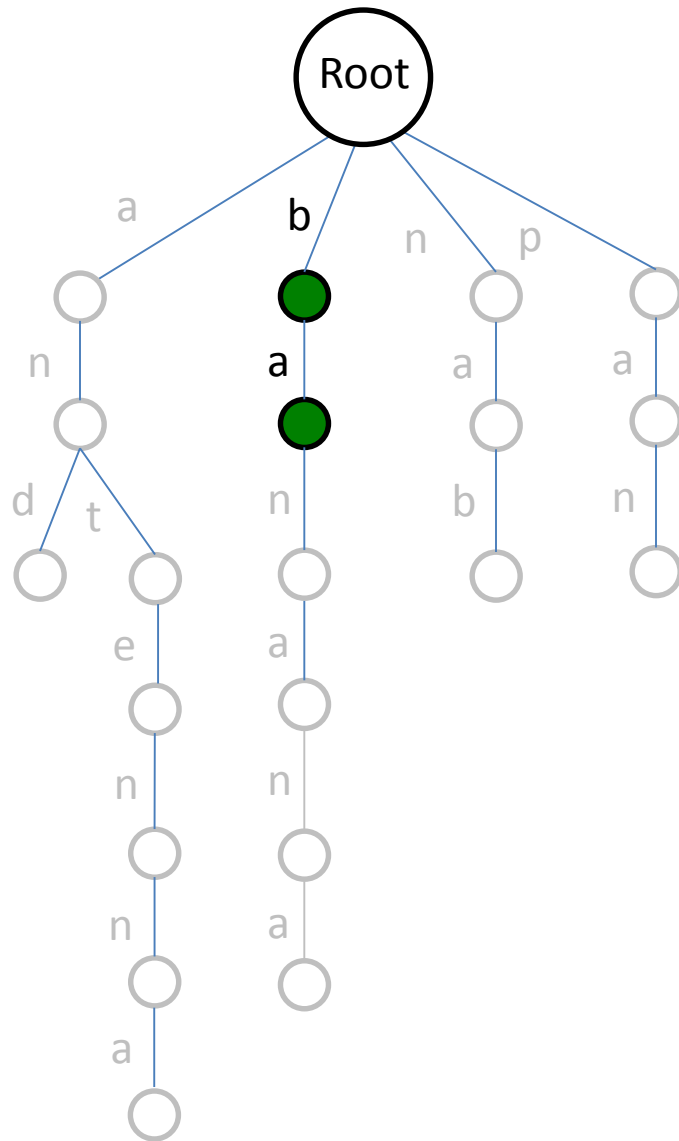
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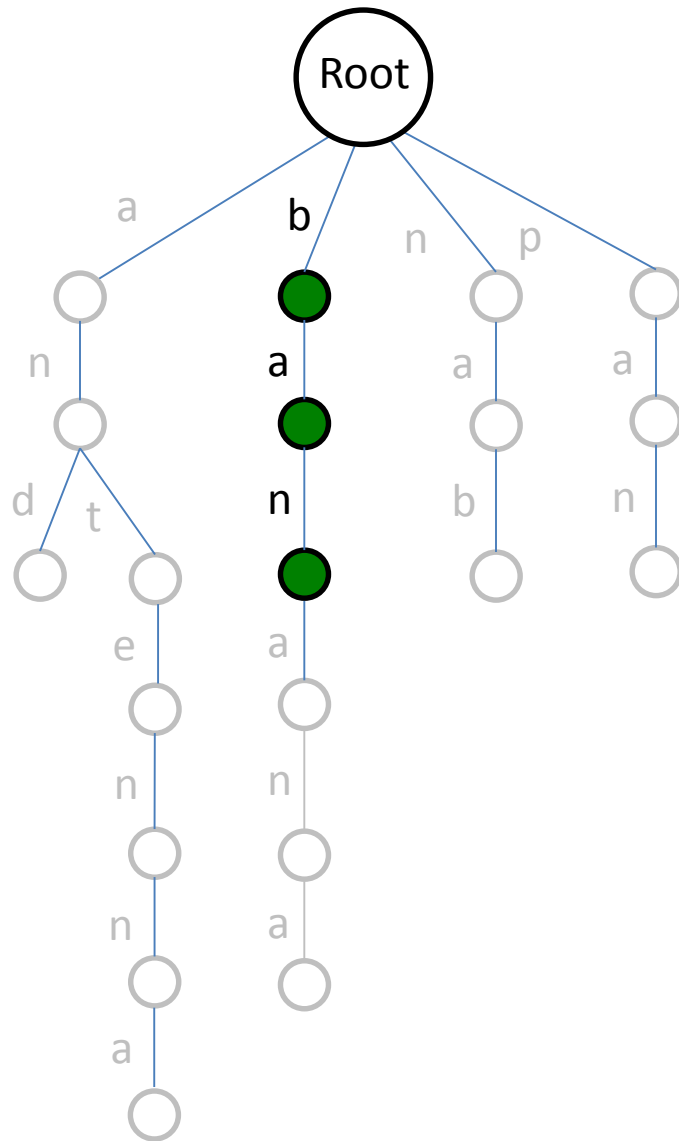
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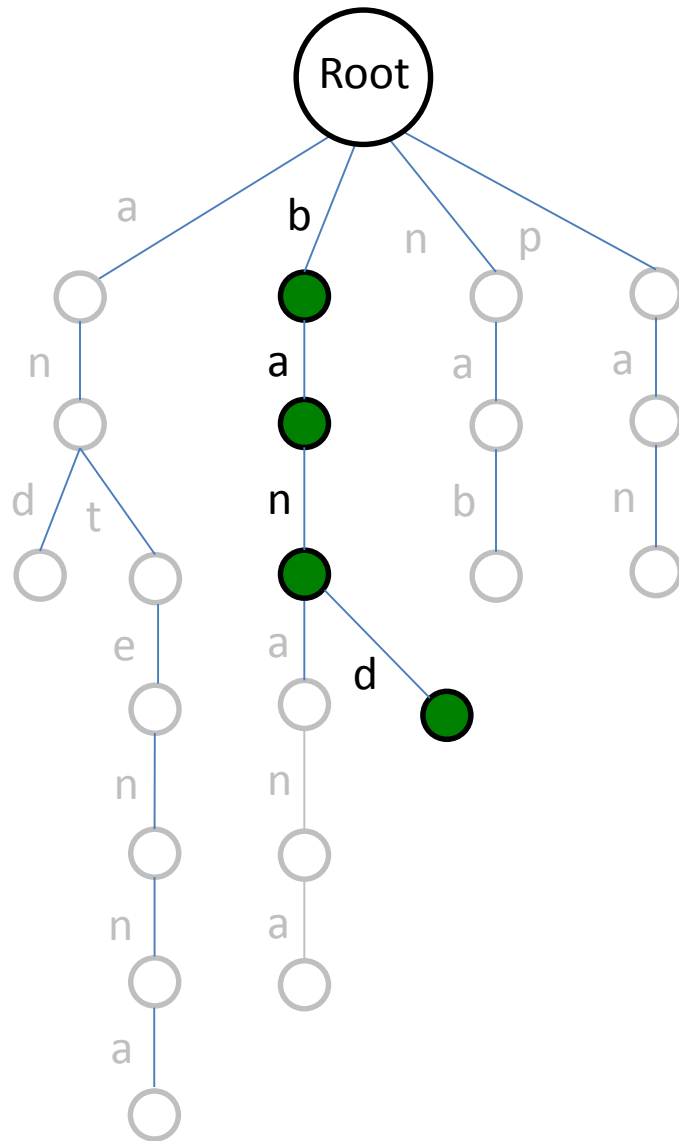
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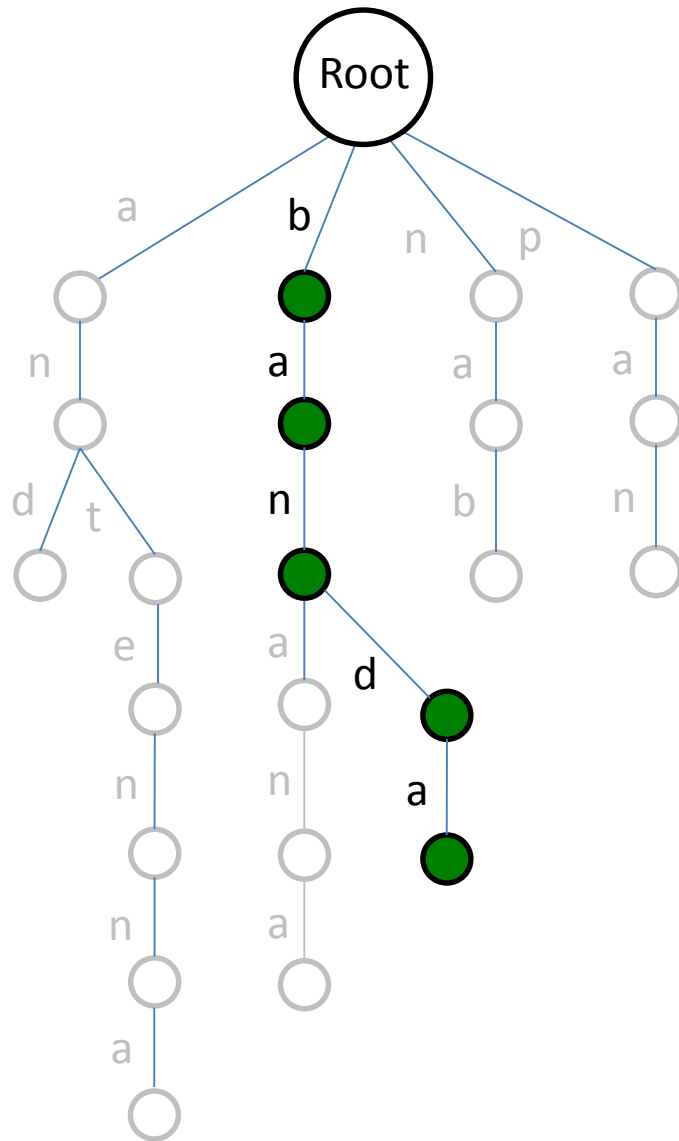
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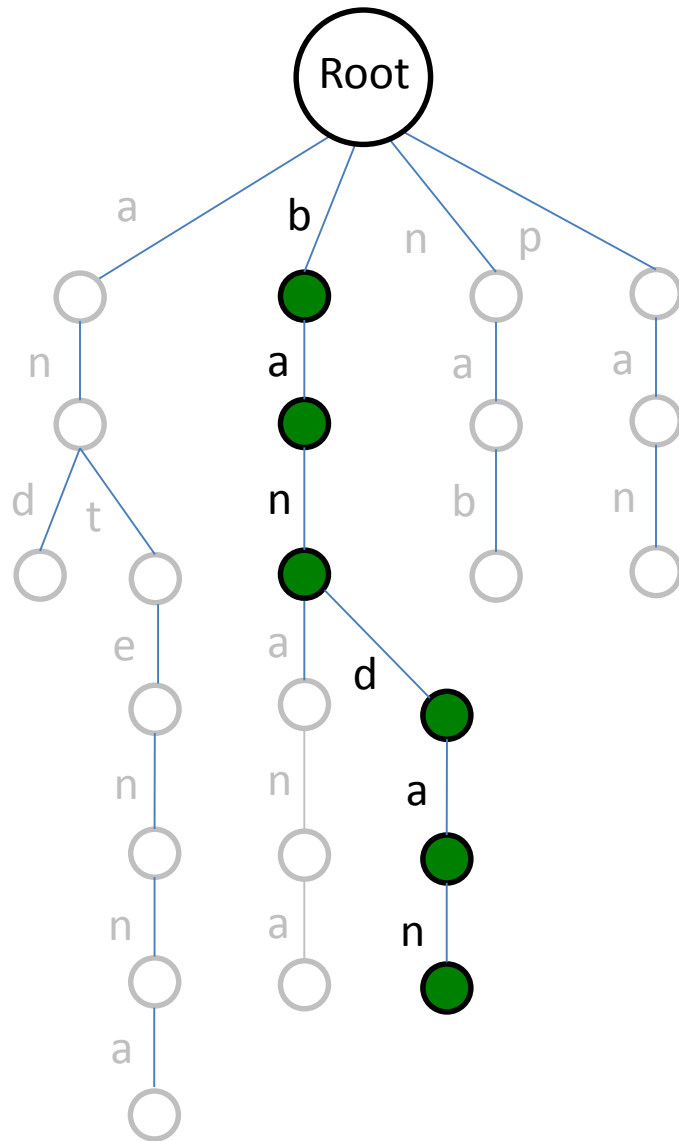
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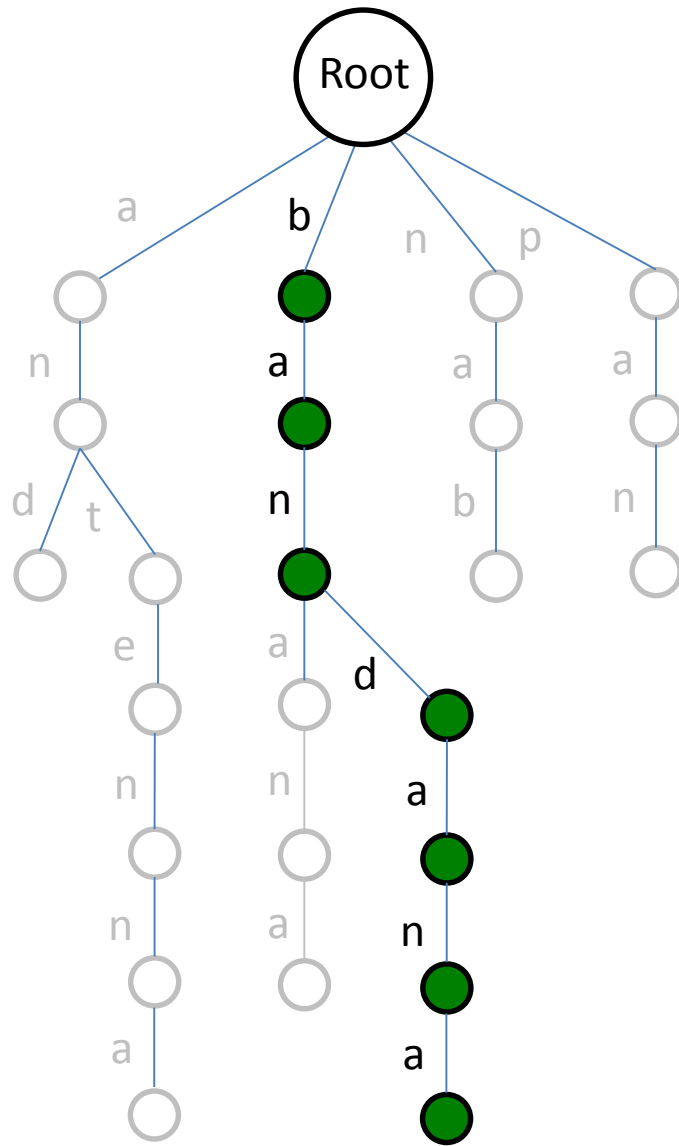
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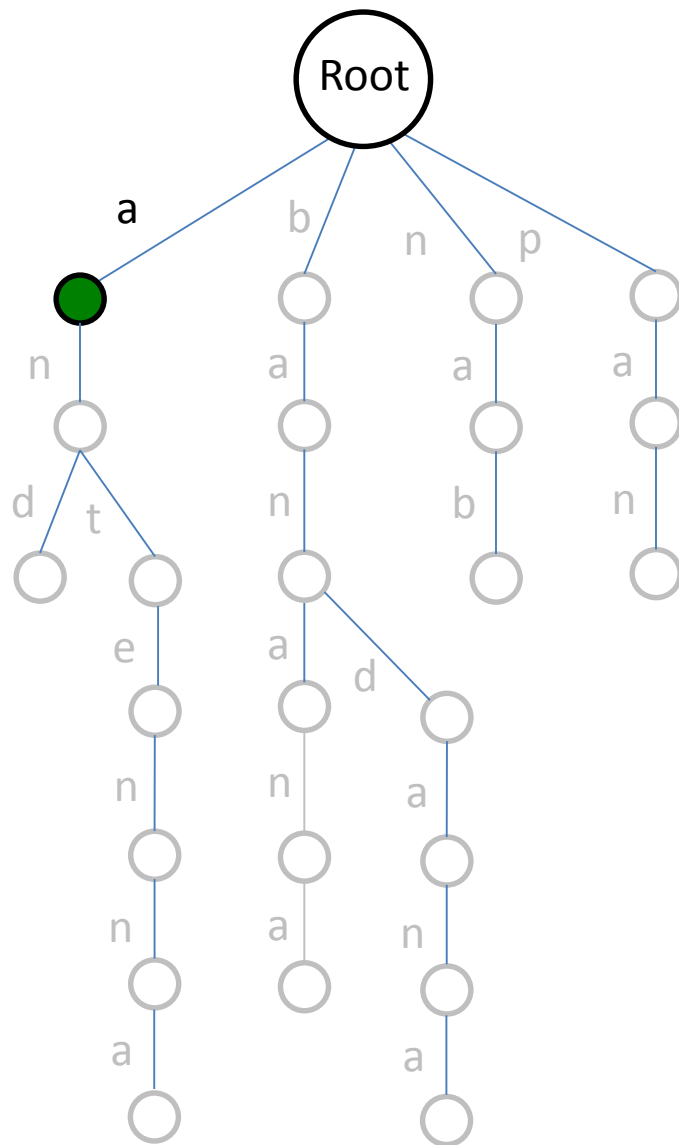
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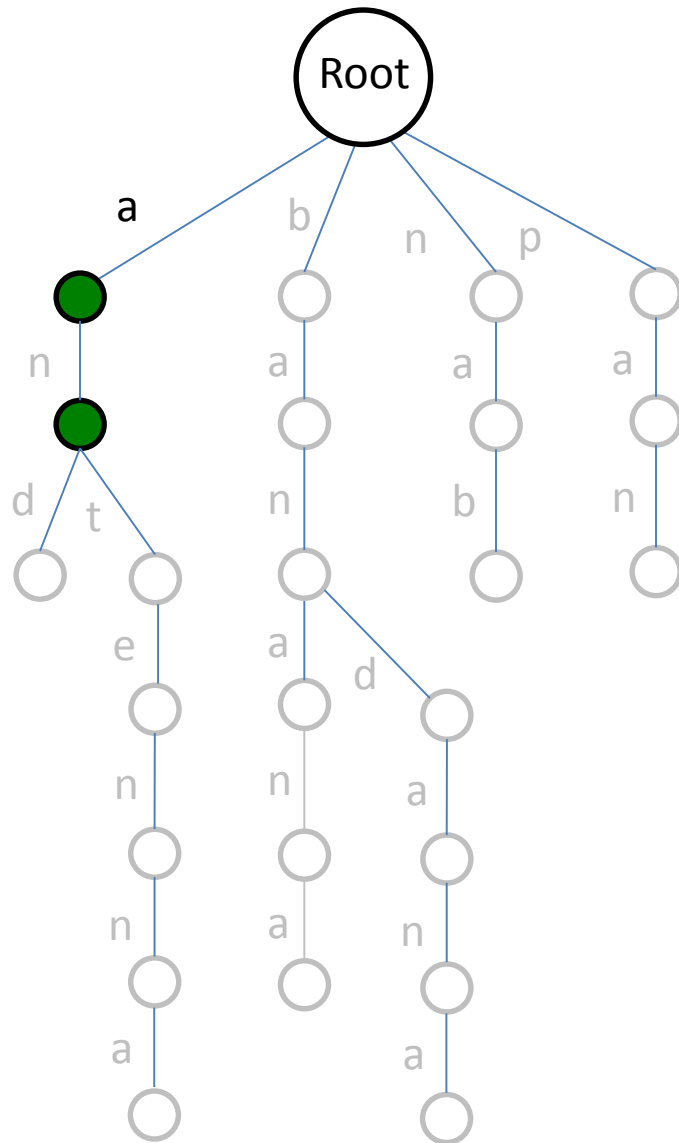
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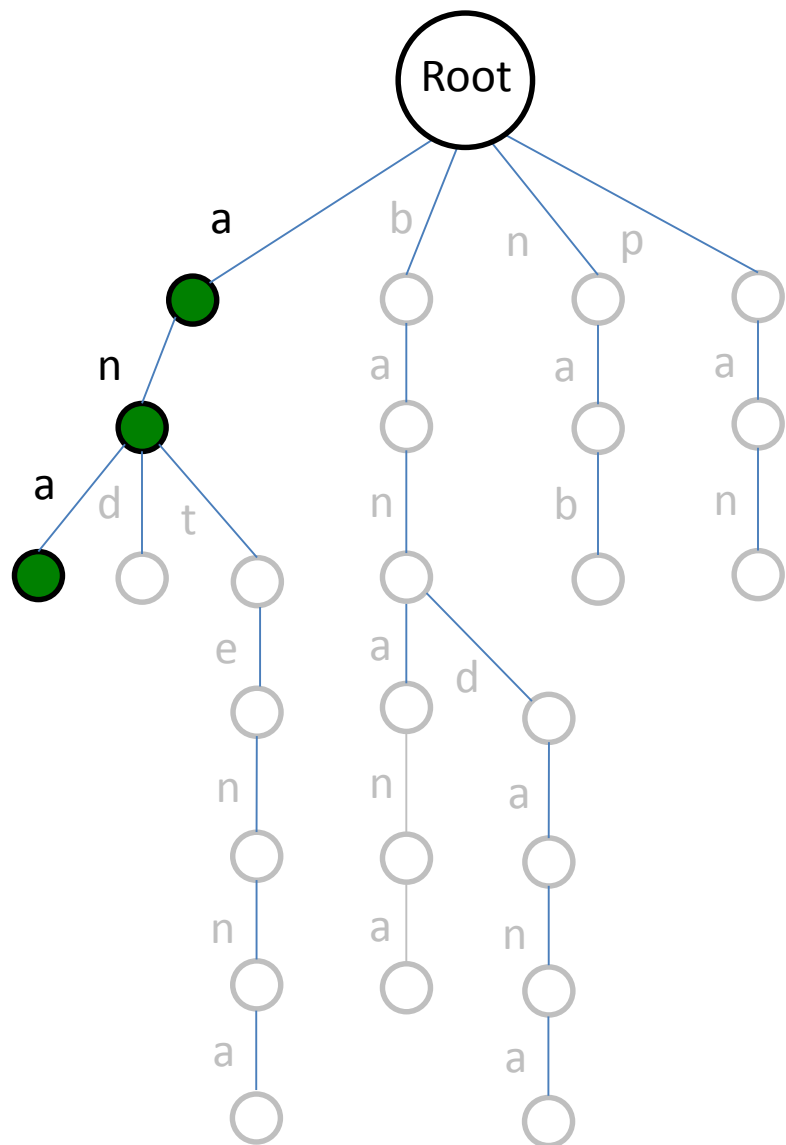
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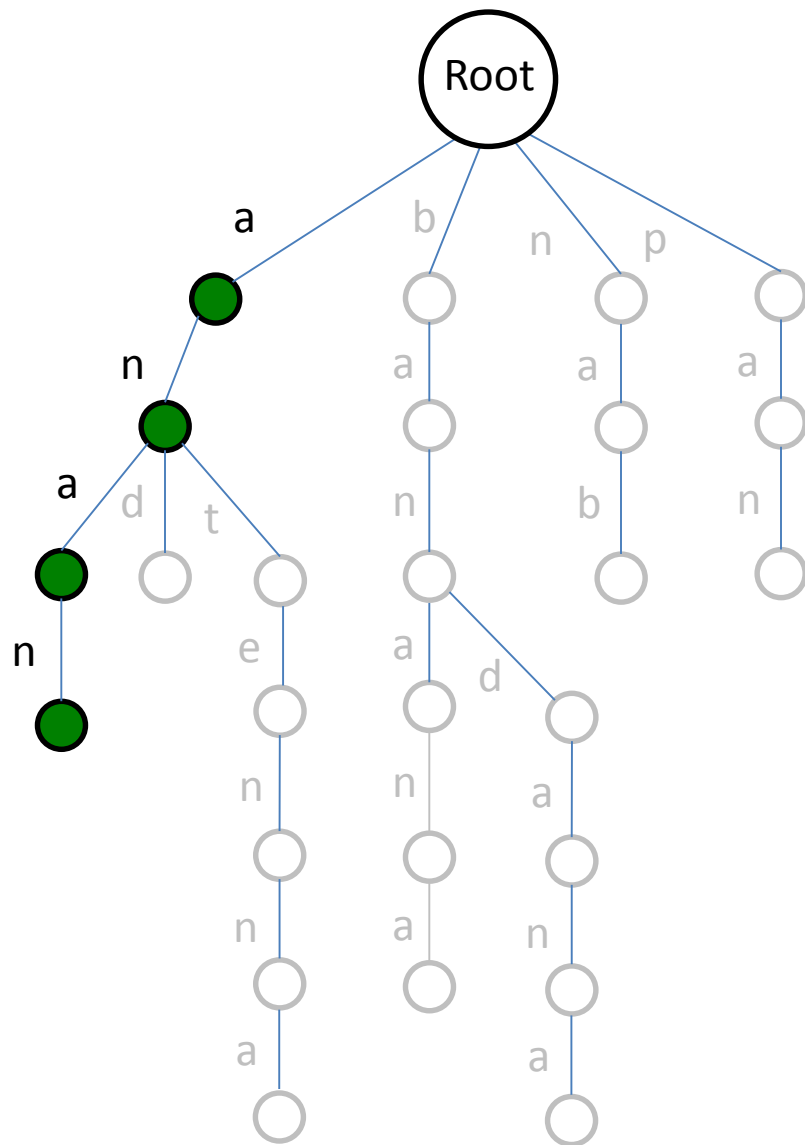
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bandana

ananas

nana



Patterns

banana

pan

and

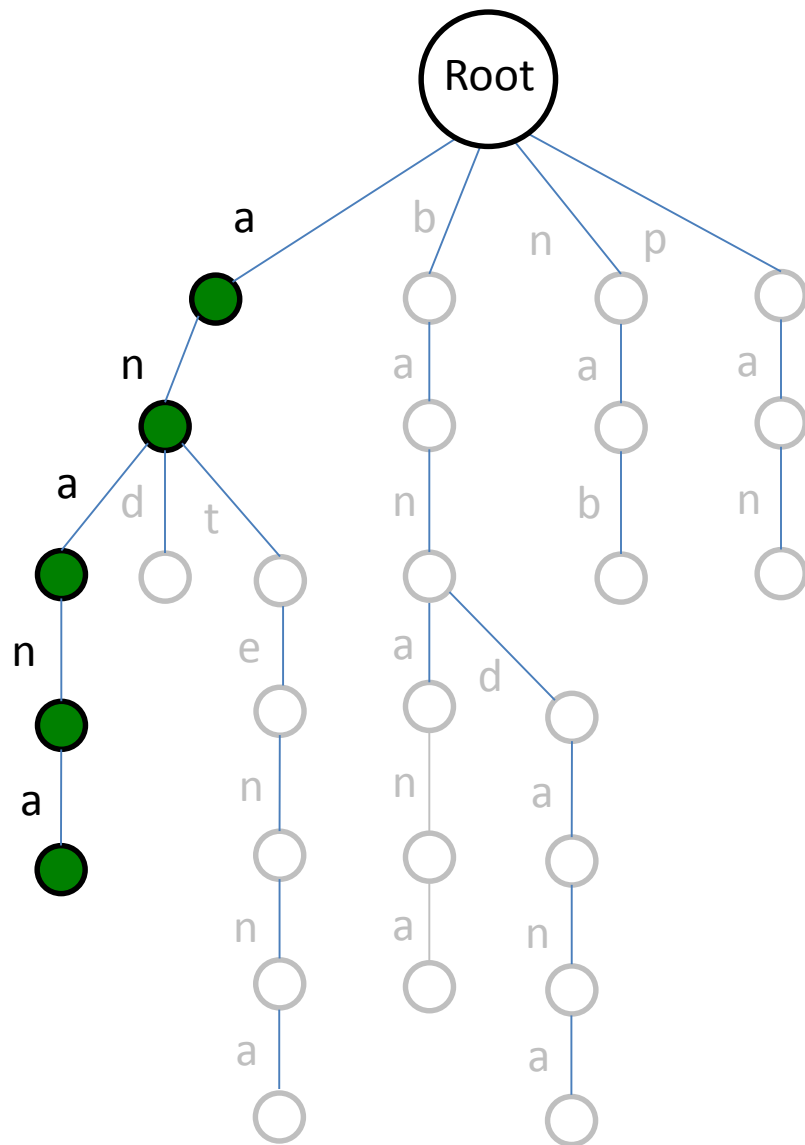
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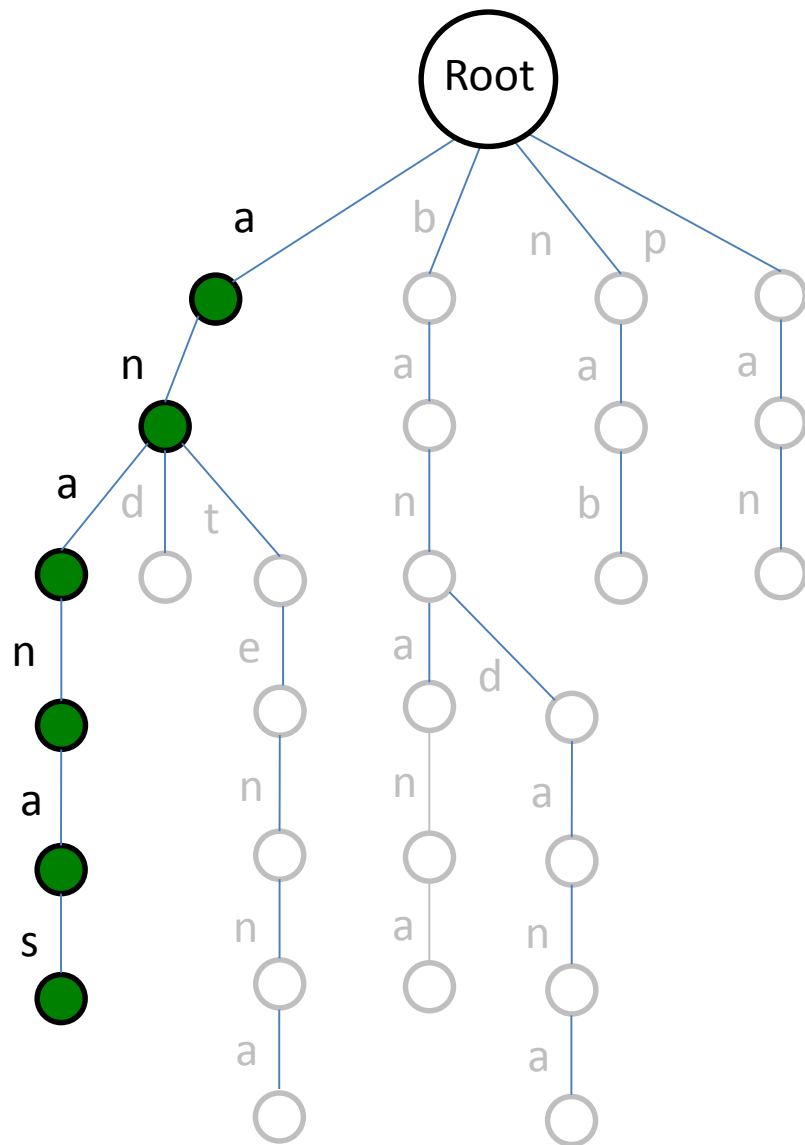
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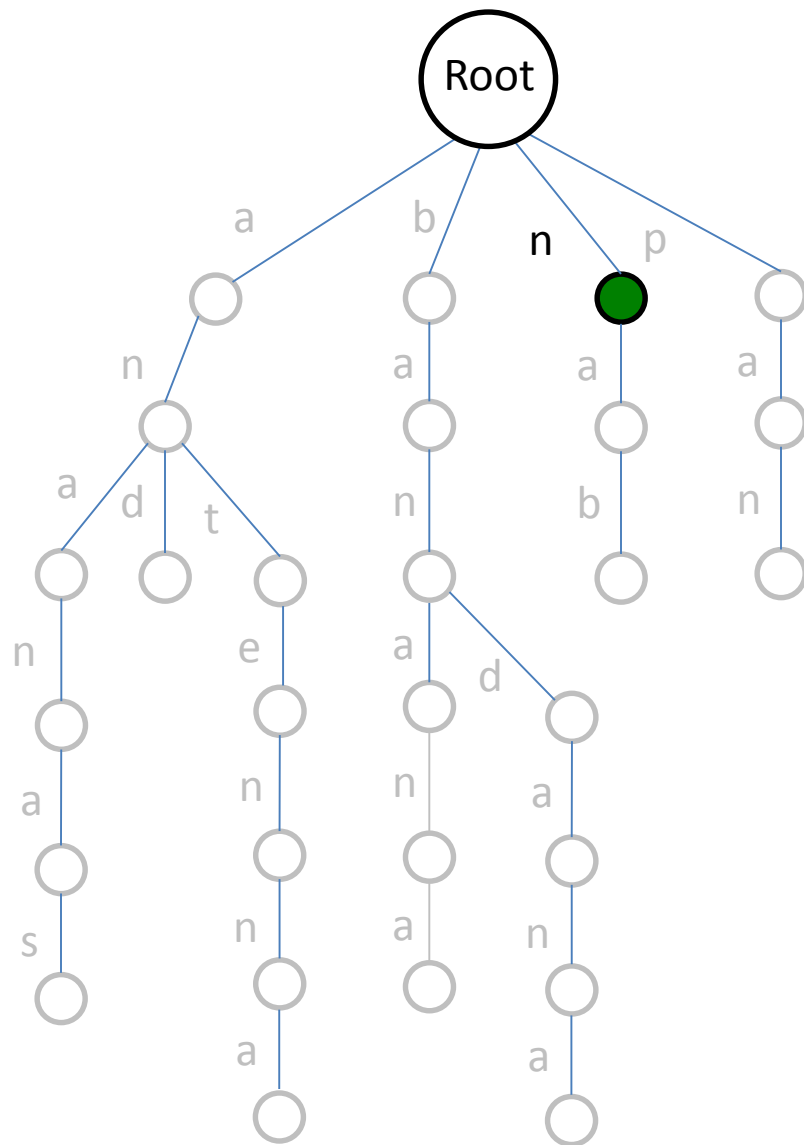
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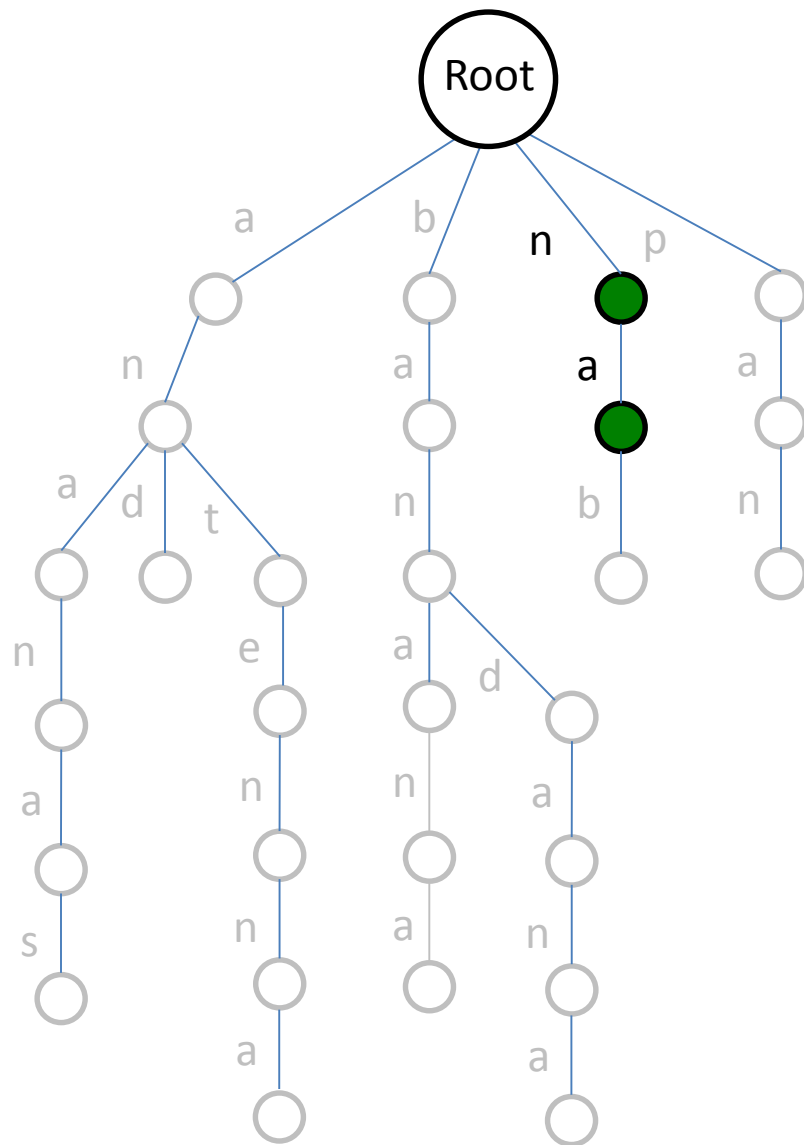
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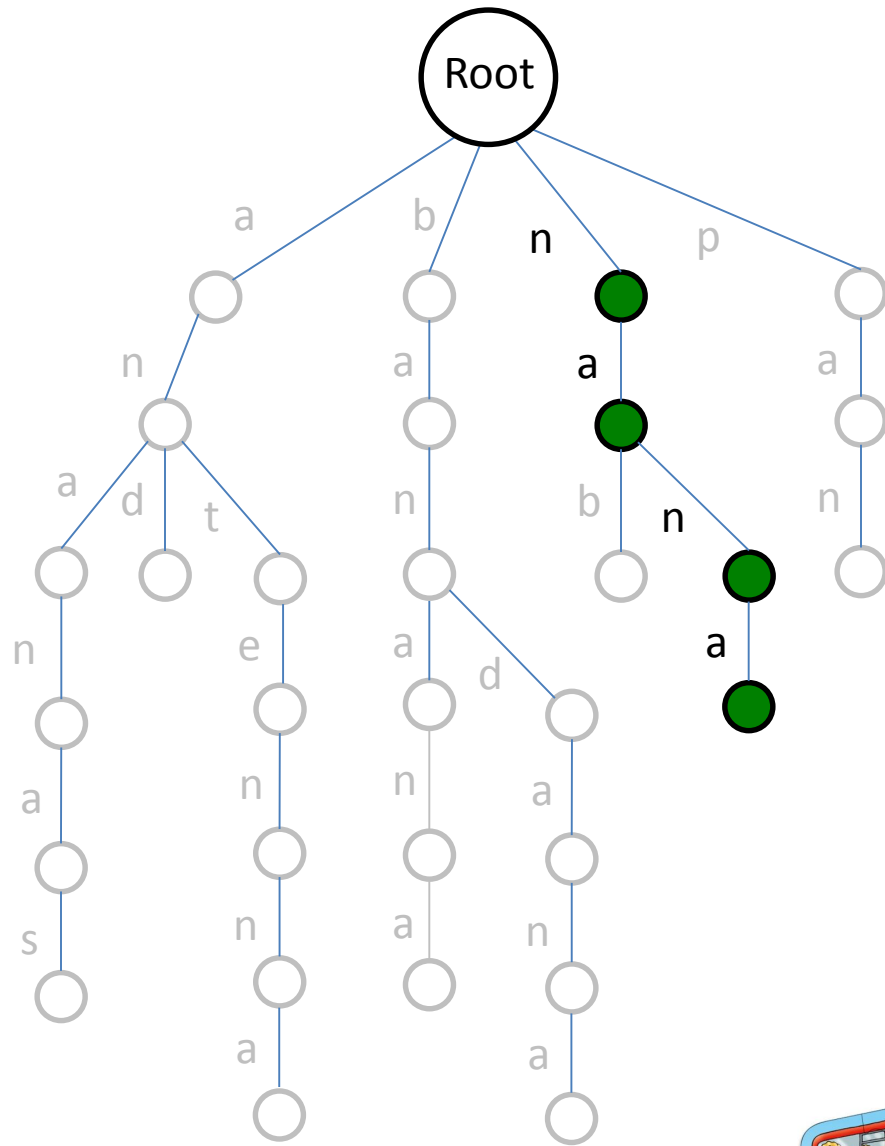
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Trie(Patterns)

Patterns

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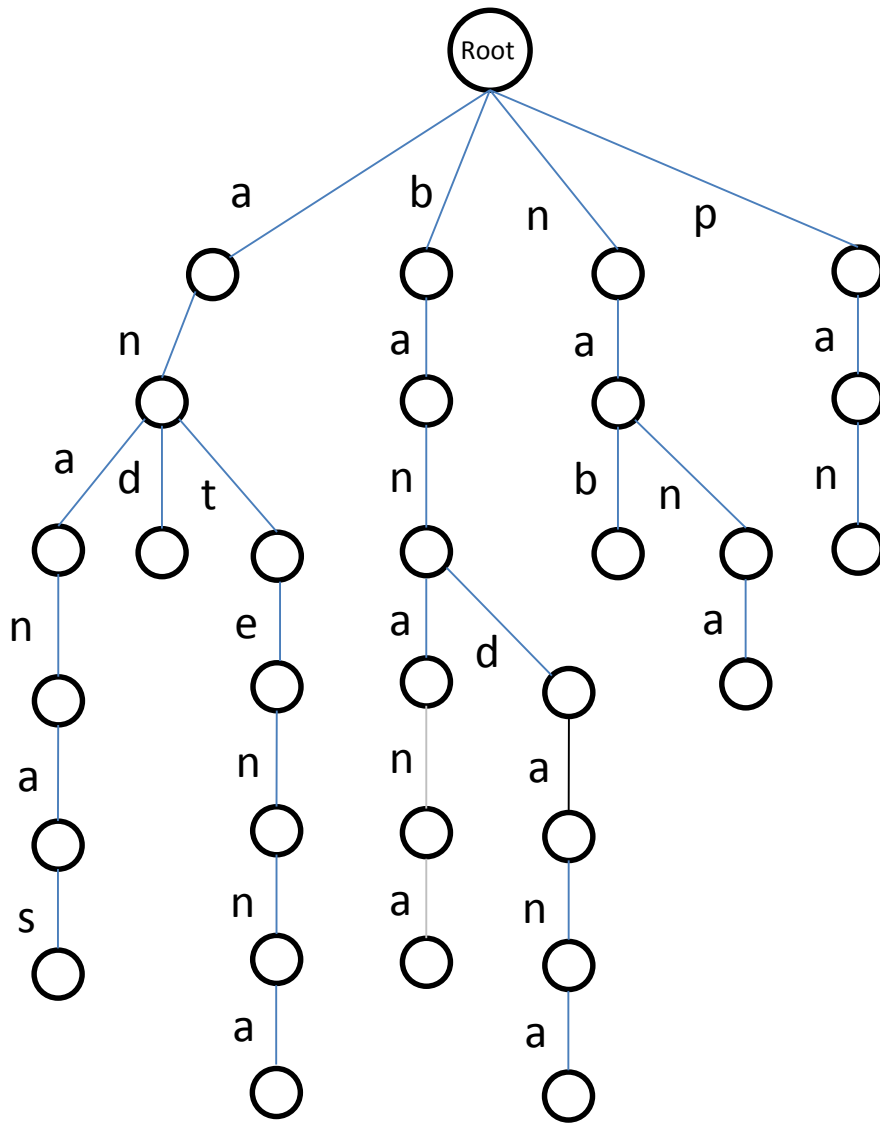
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TrieMatching(*Text*, *Patterns*):
drive Trie(*Patterns*) along *Text*
at each position of *Text*

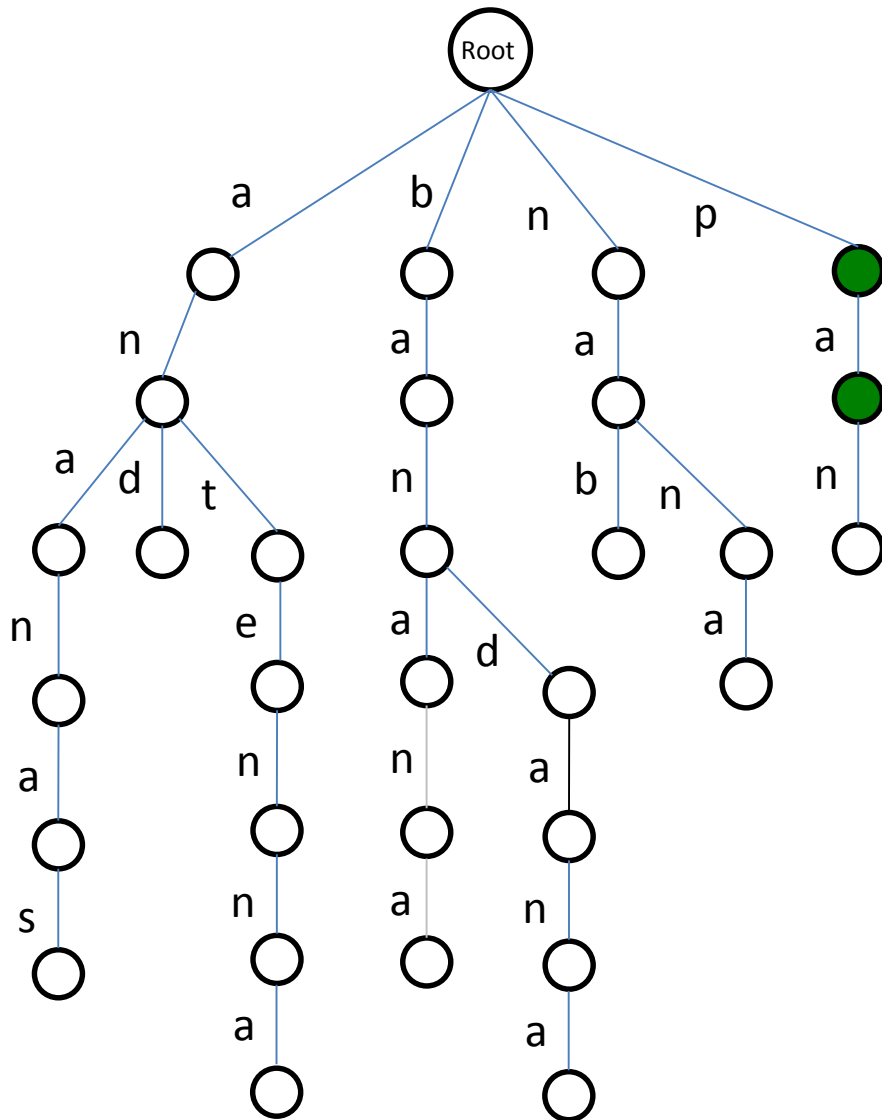
- walk down Trie(*Patterns*) by spelling symbols of *Text*
- a pattern from *Patterns* matches *Text* each time you reach a leaf!

For simplicity, we assume that no pattern is a substring of another pattern

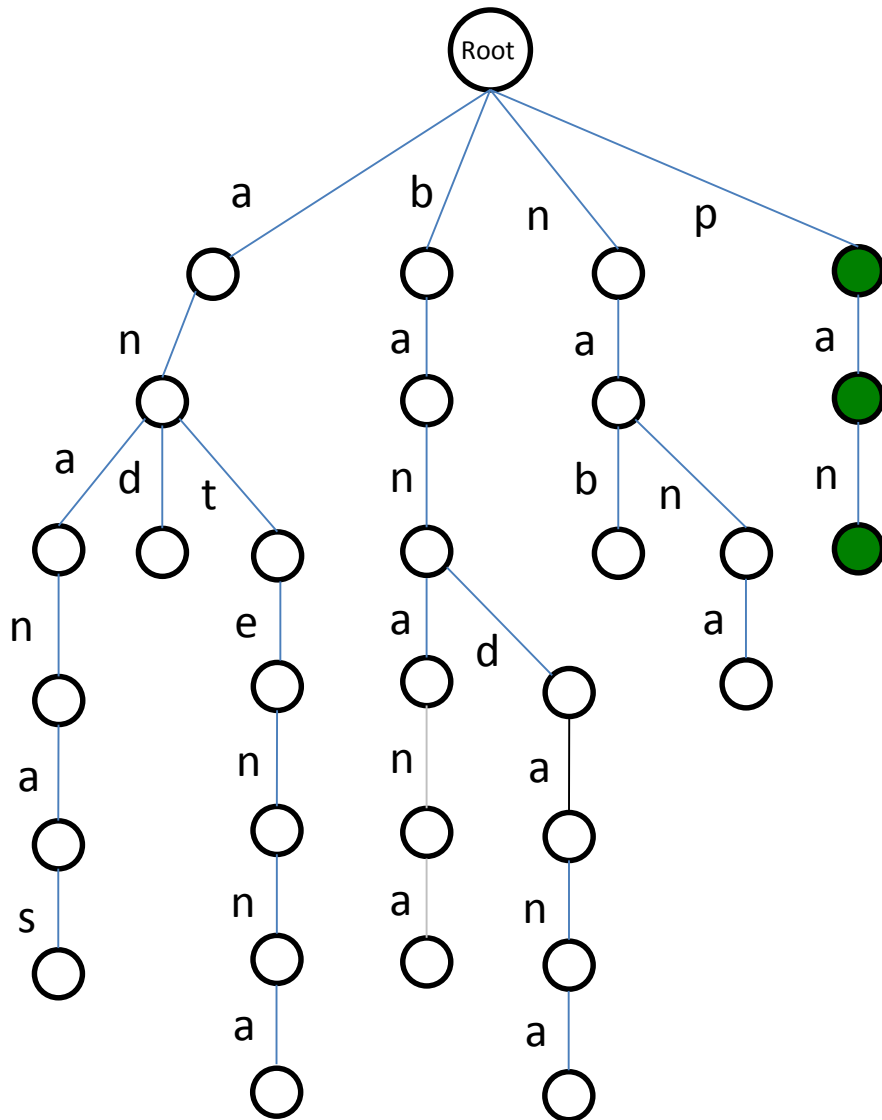
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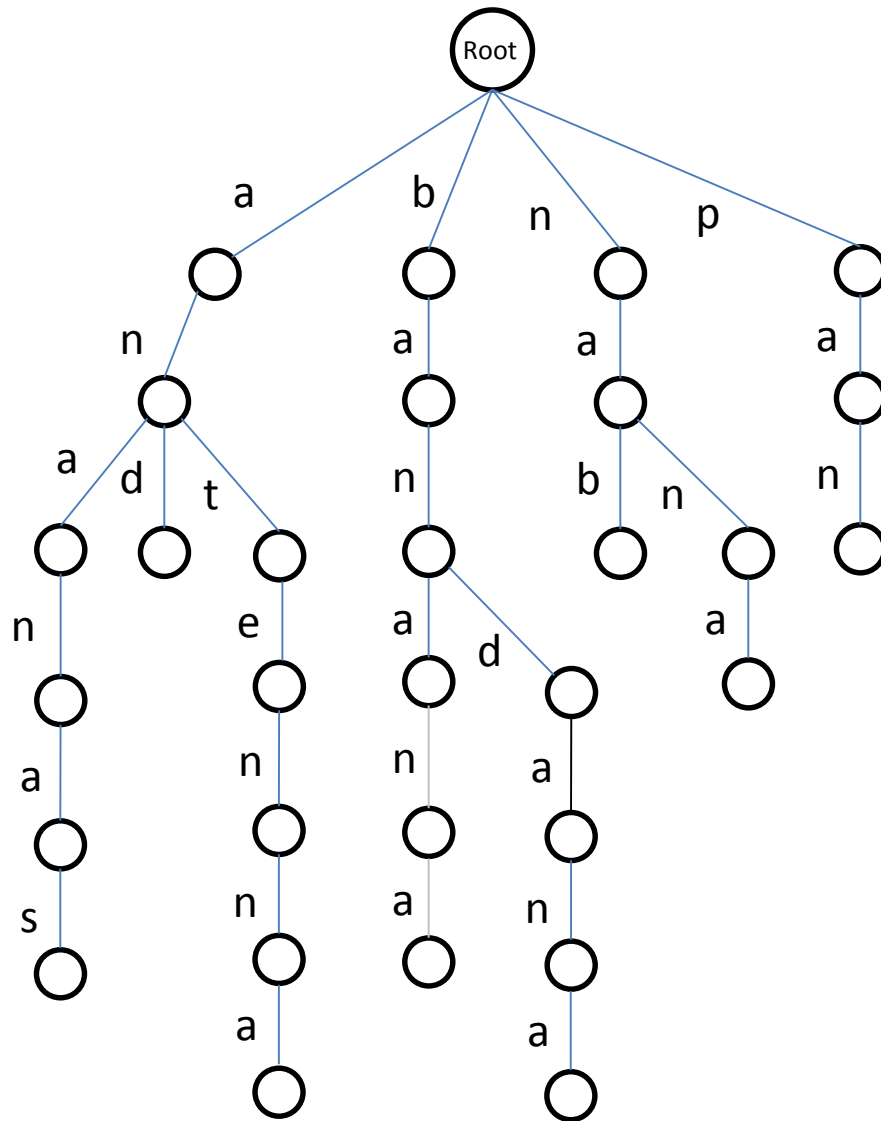
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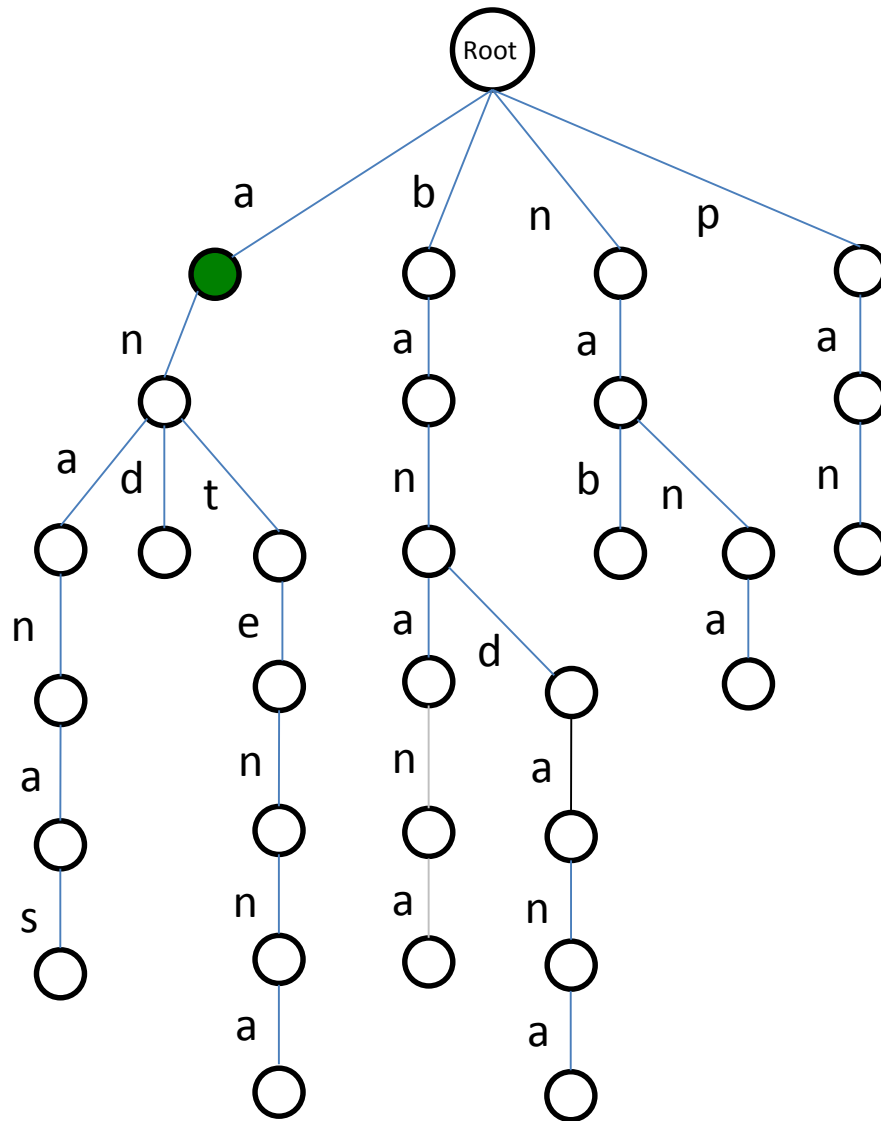
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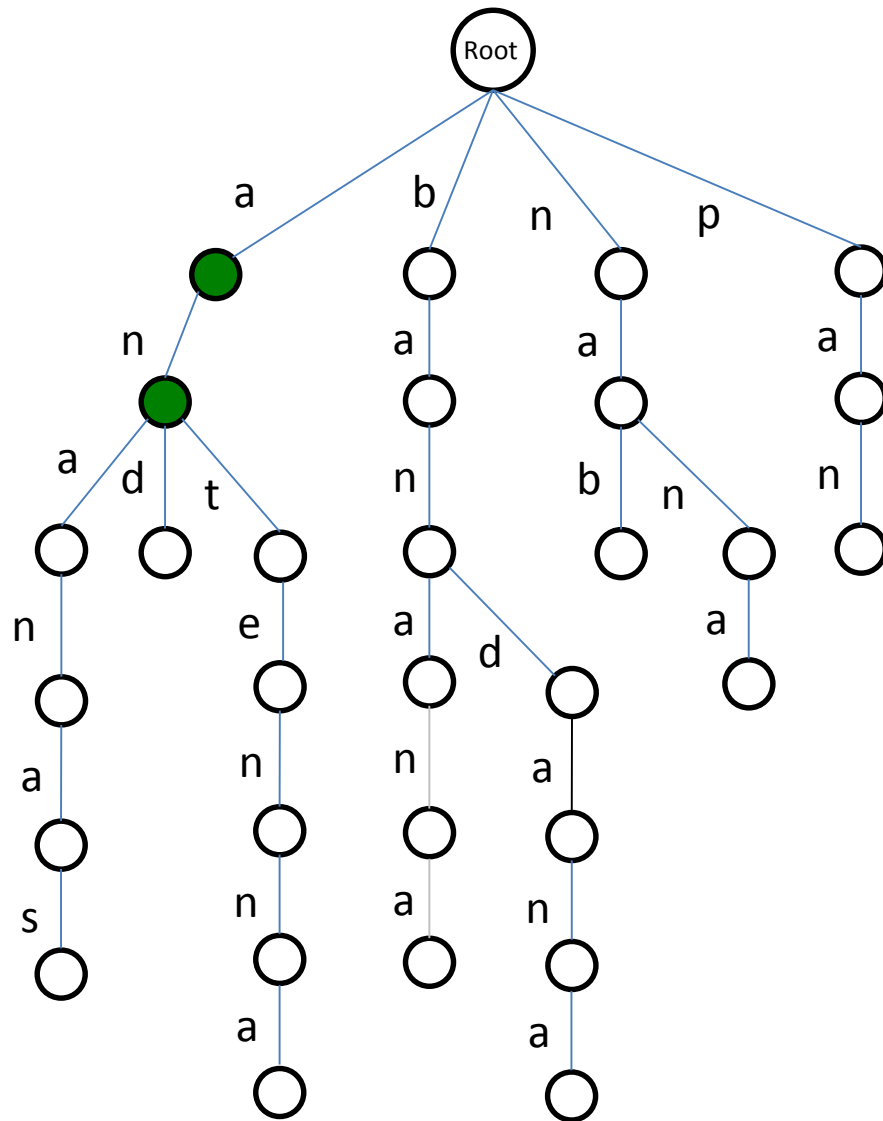
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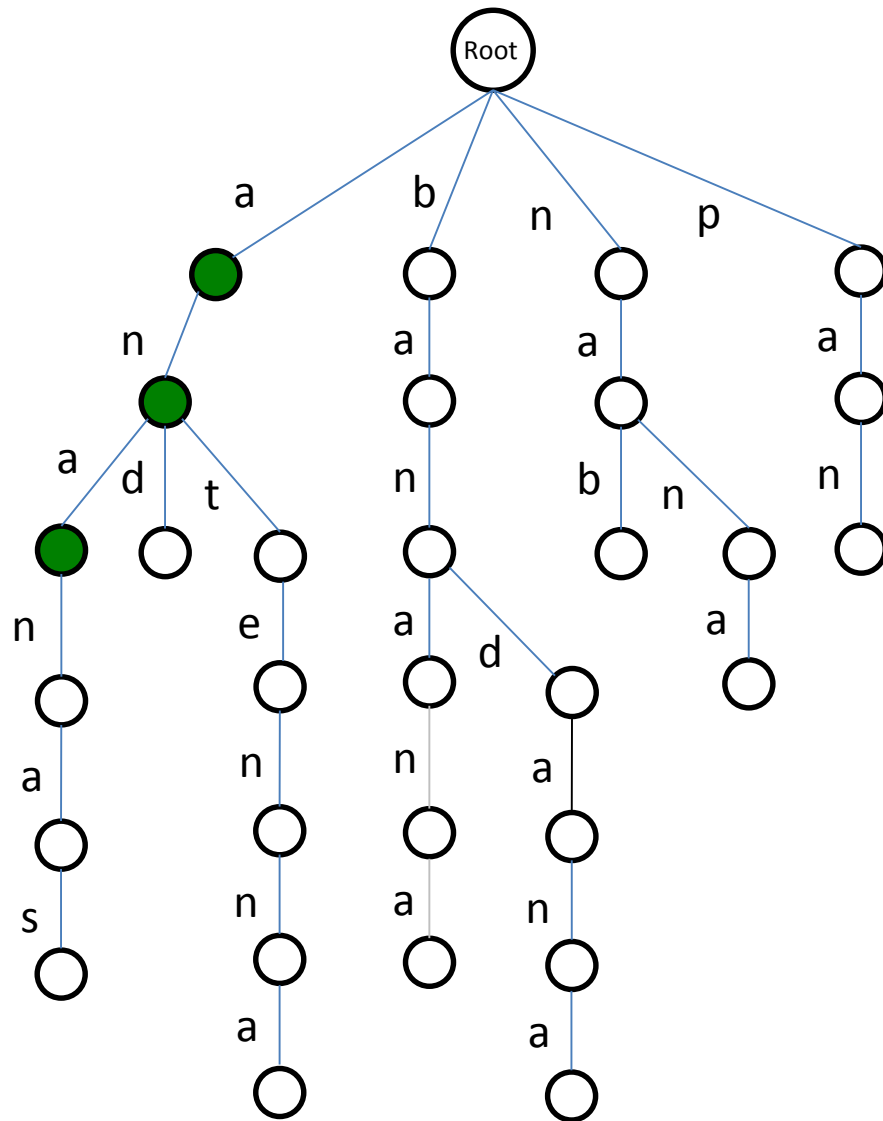
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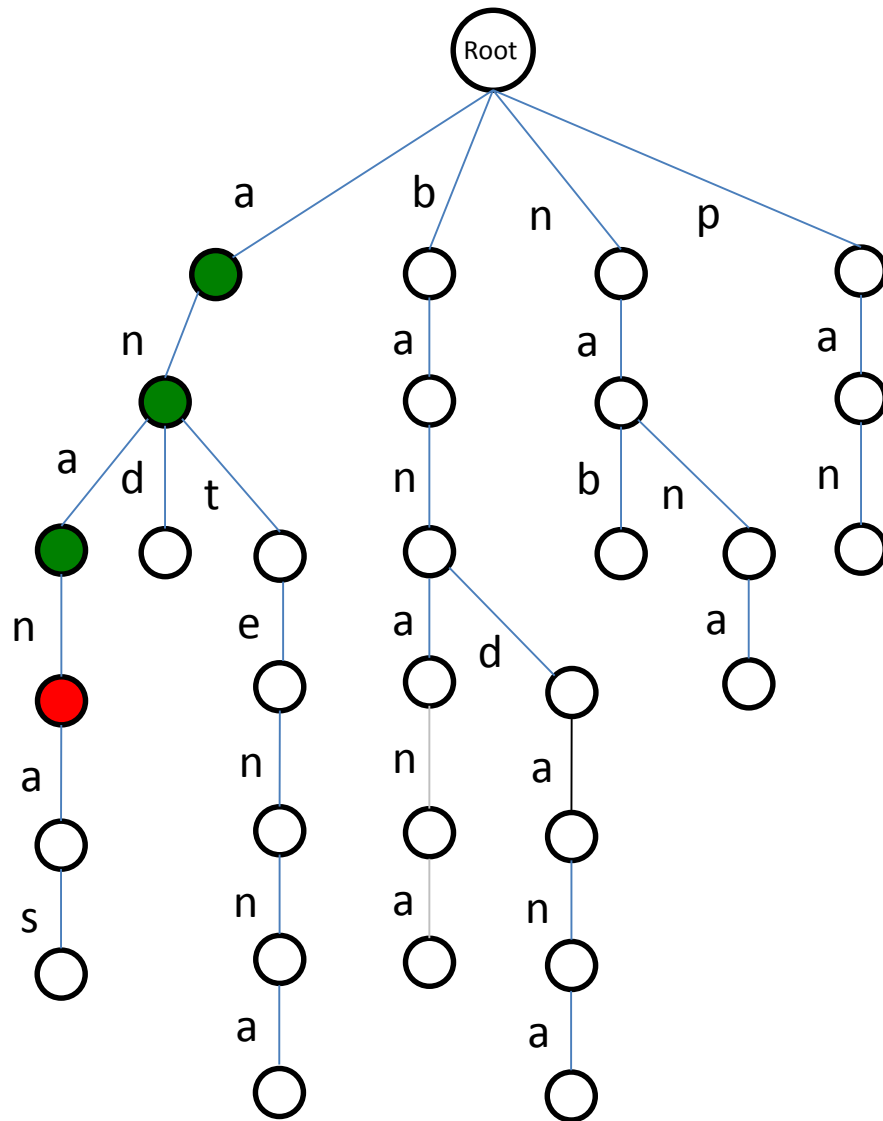
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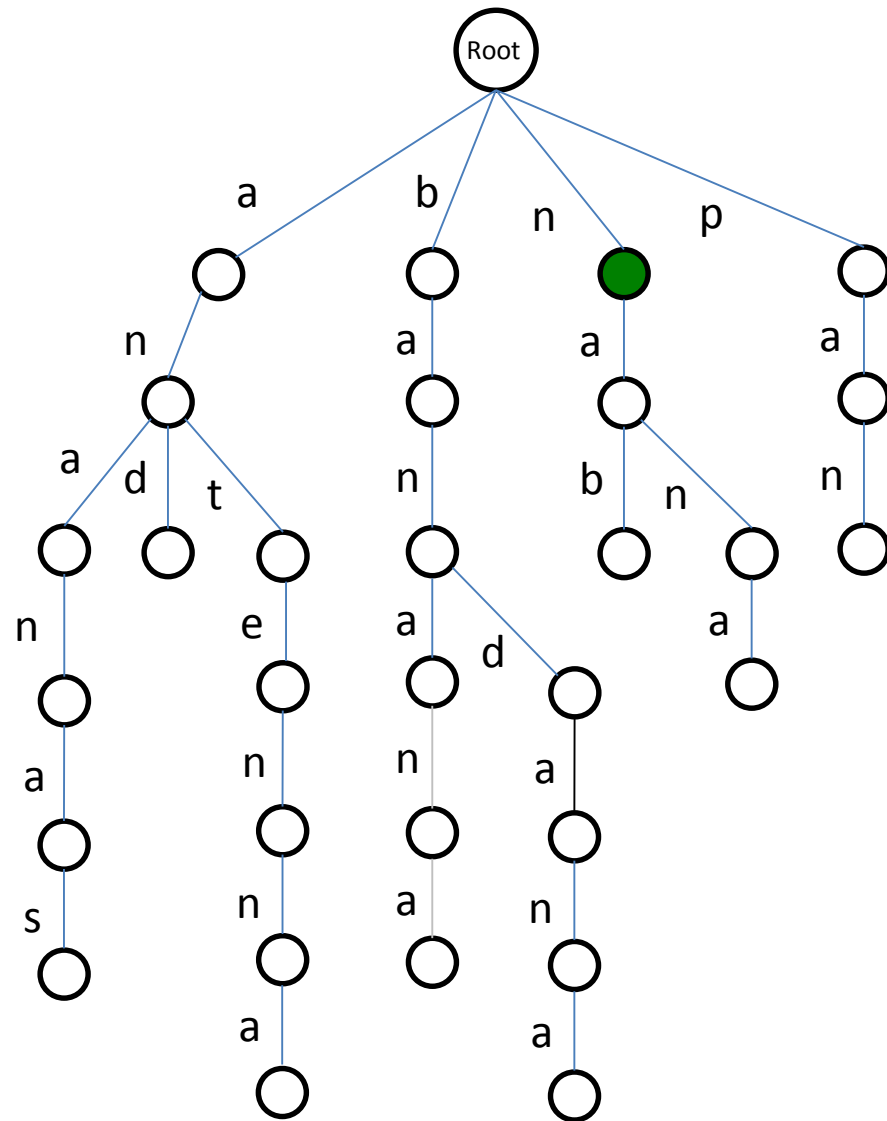
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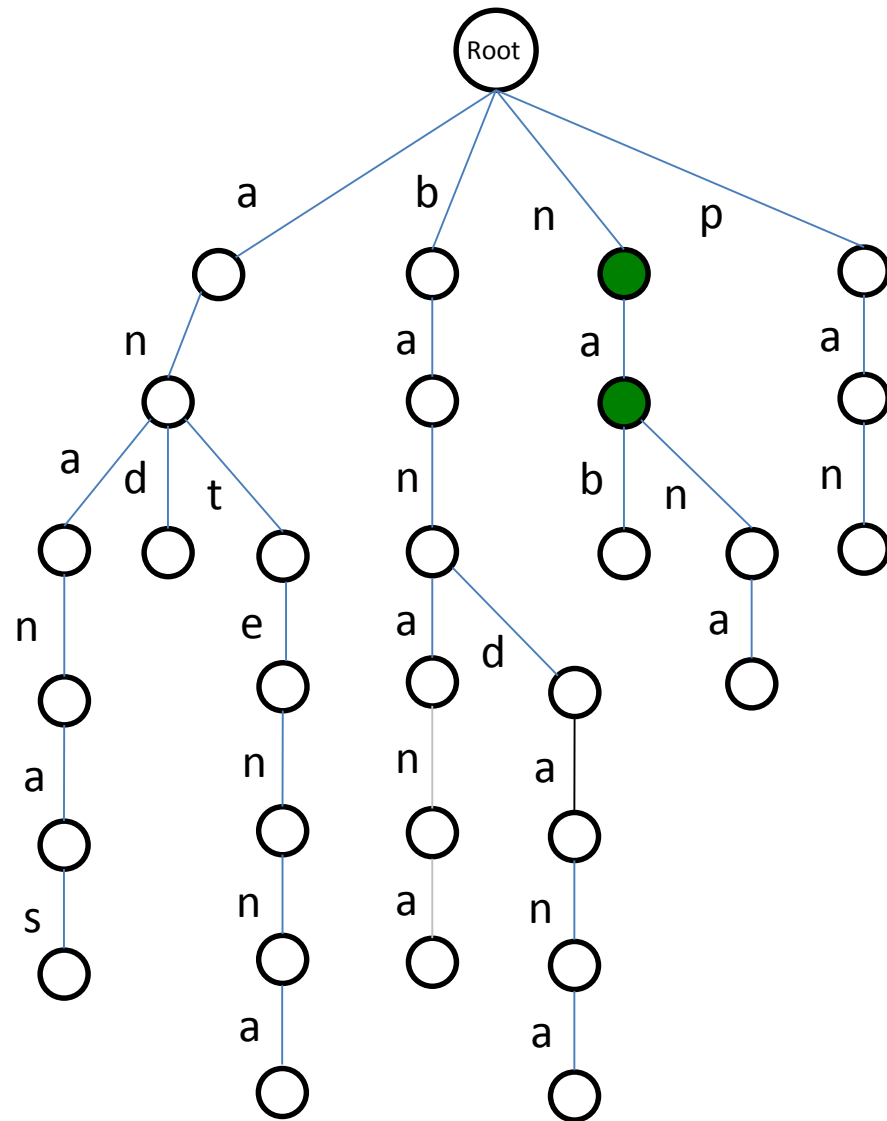
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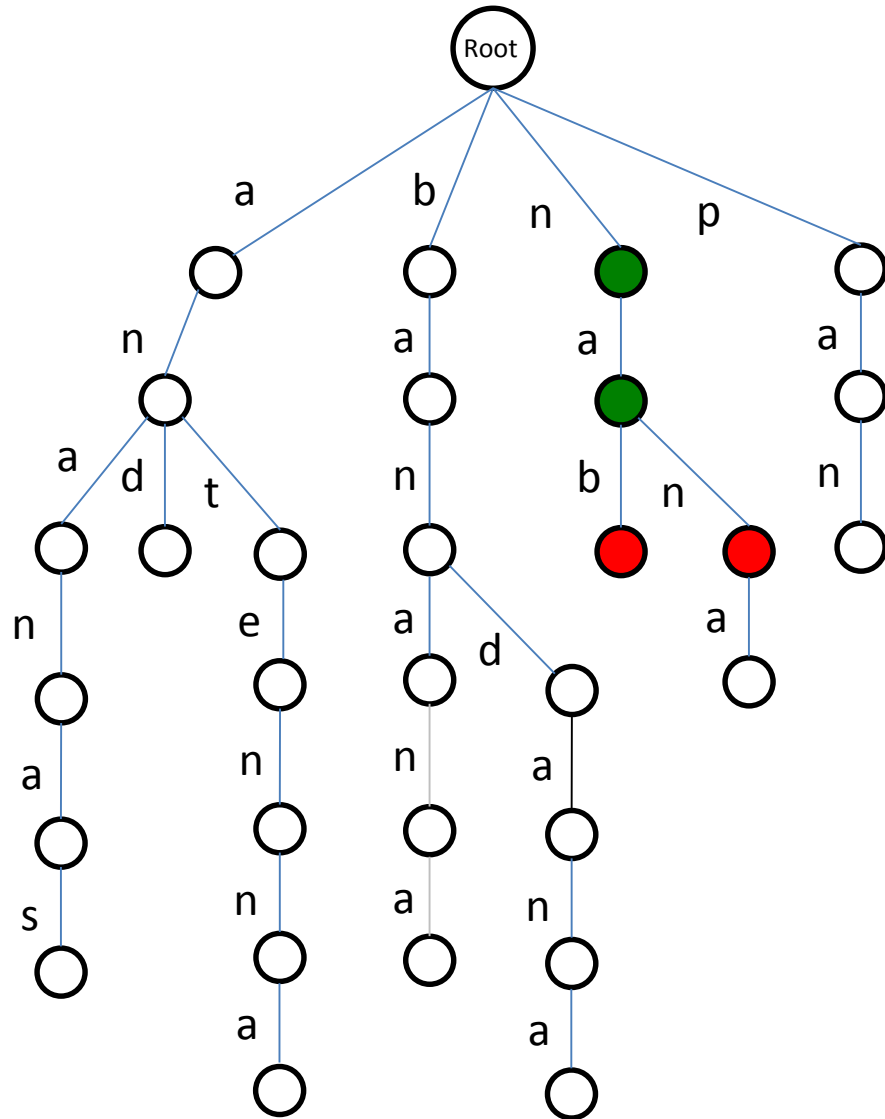
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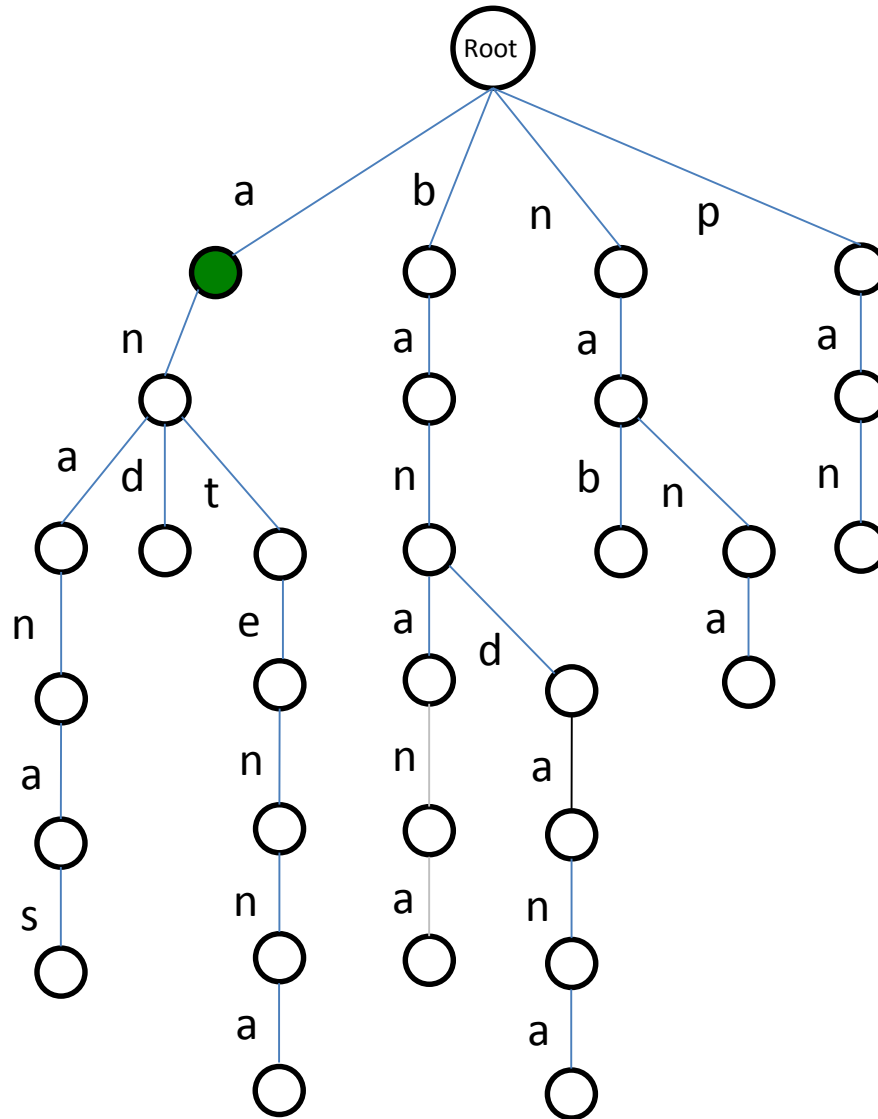
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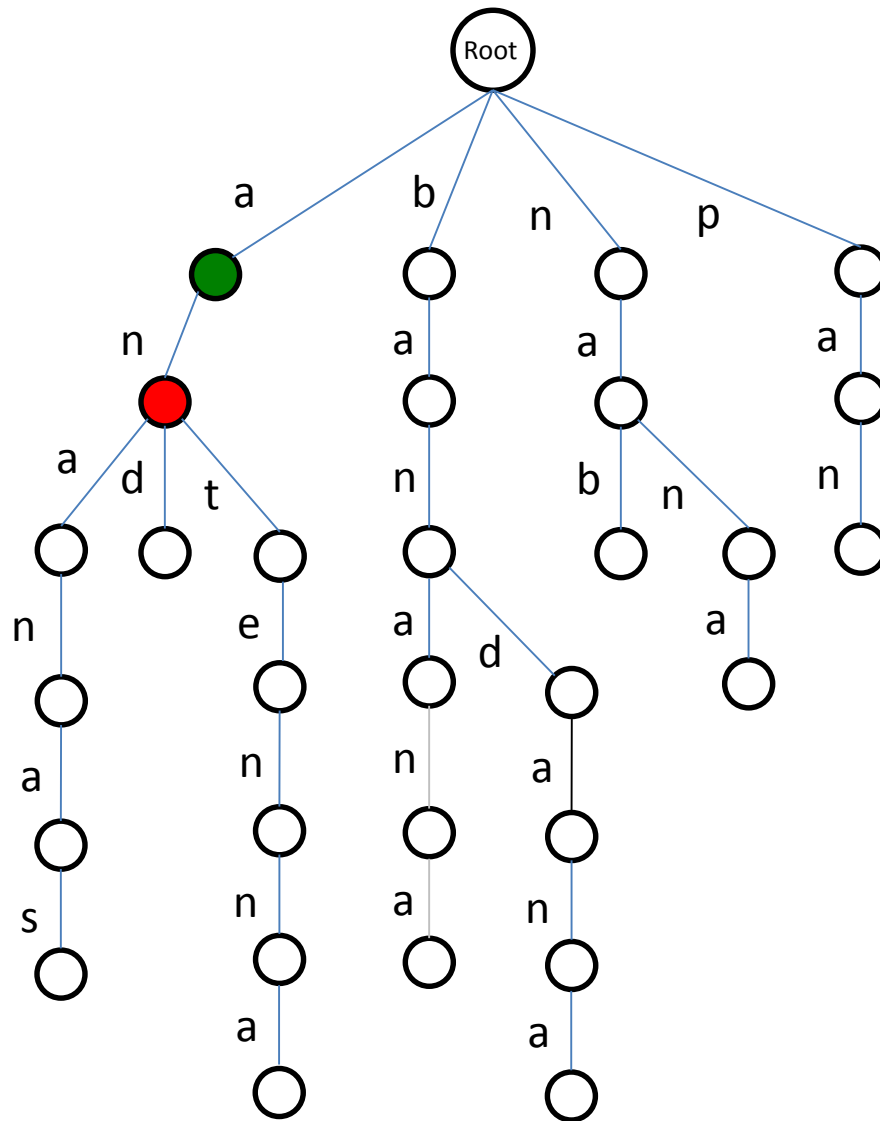
p a n a m a b a n a n a s



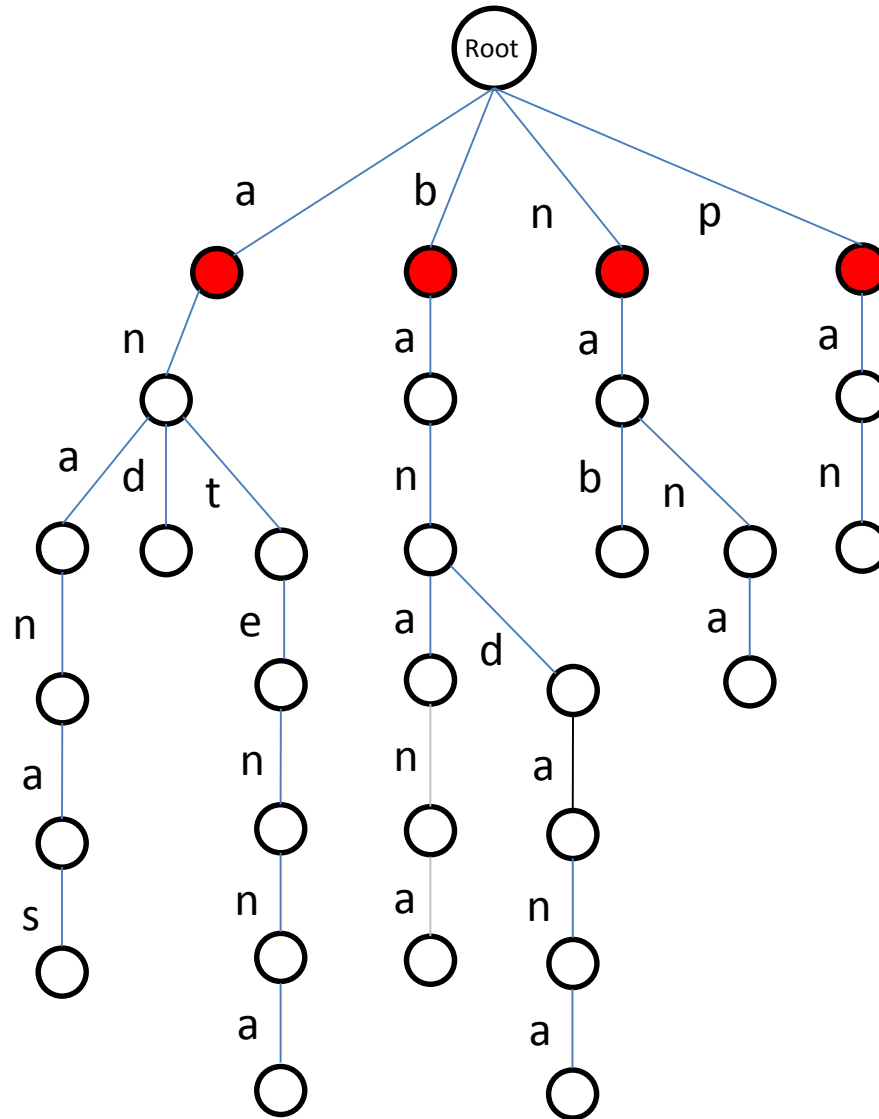
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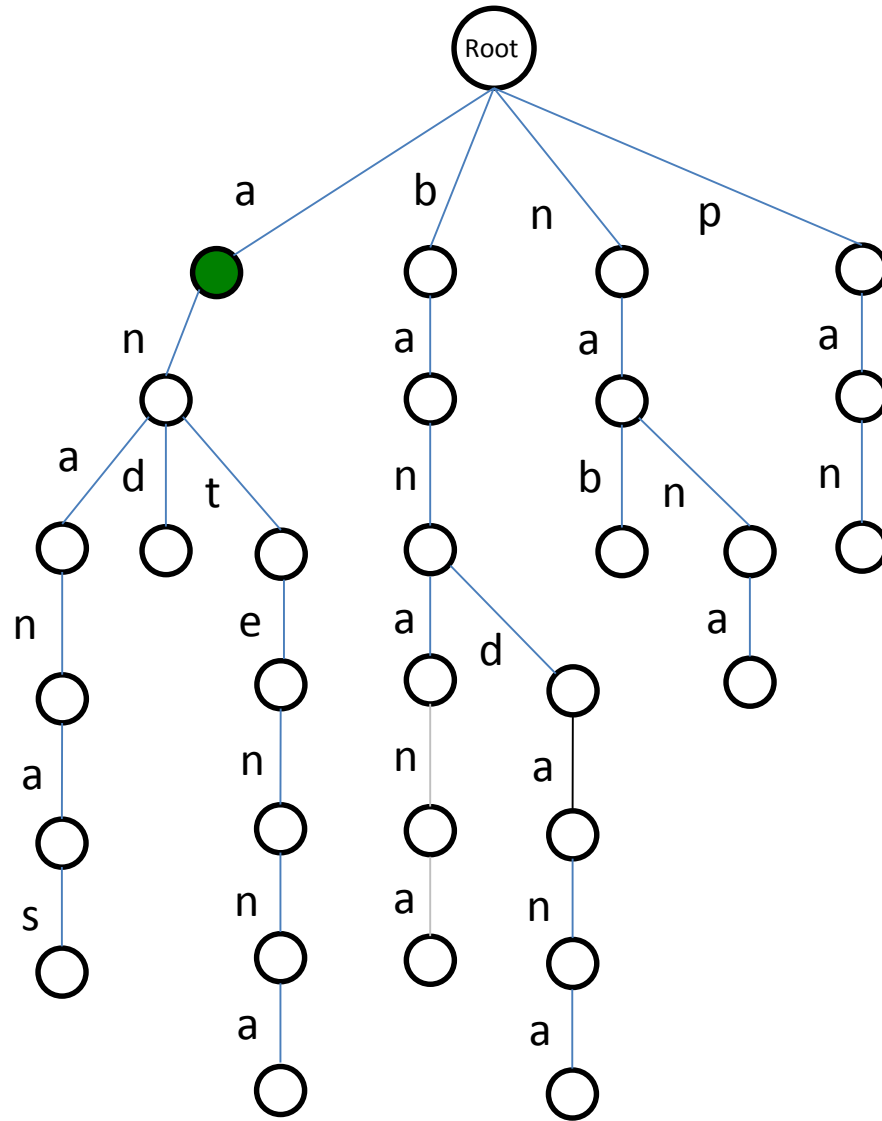
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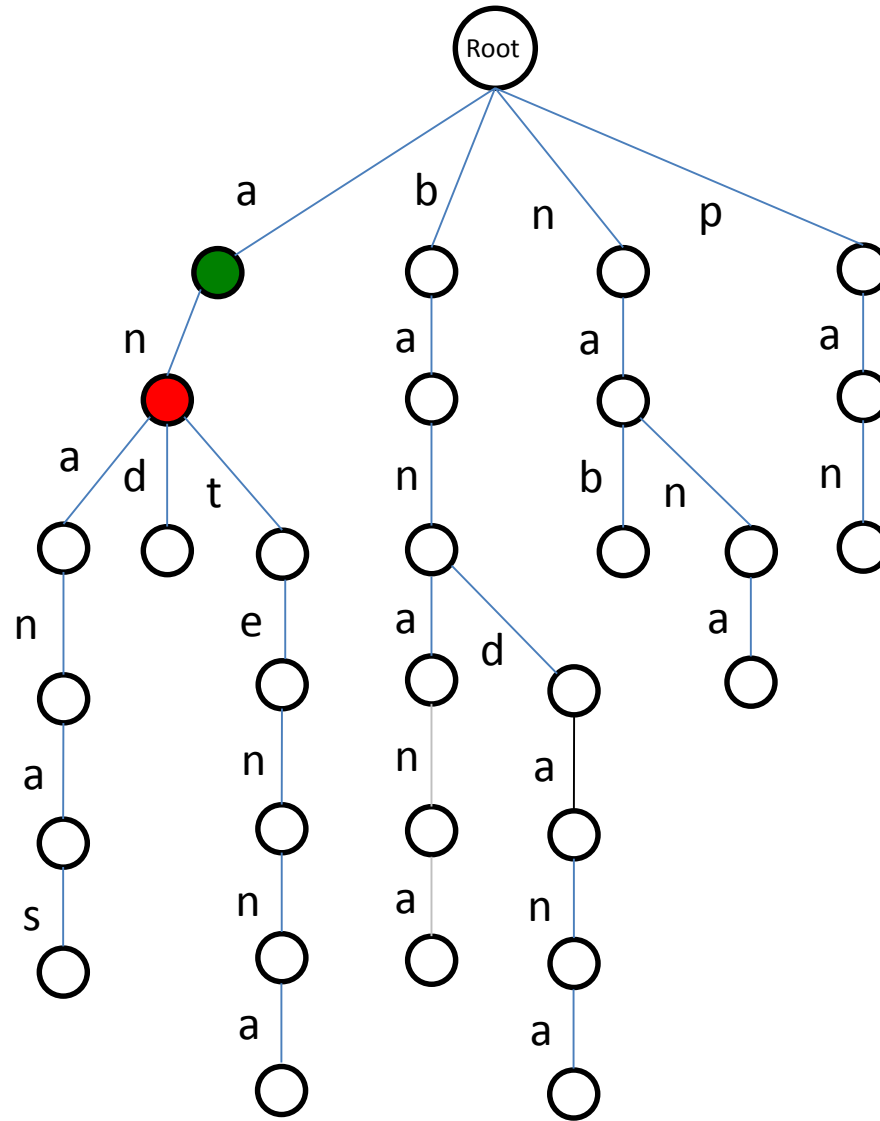
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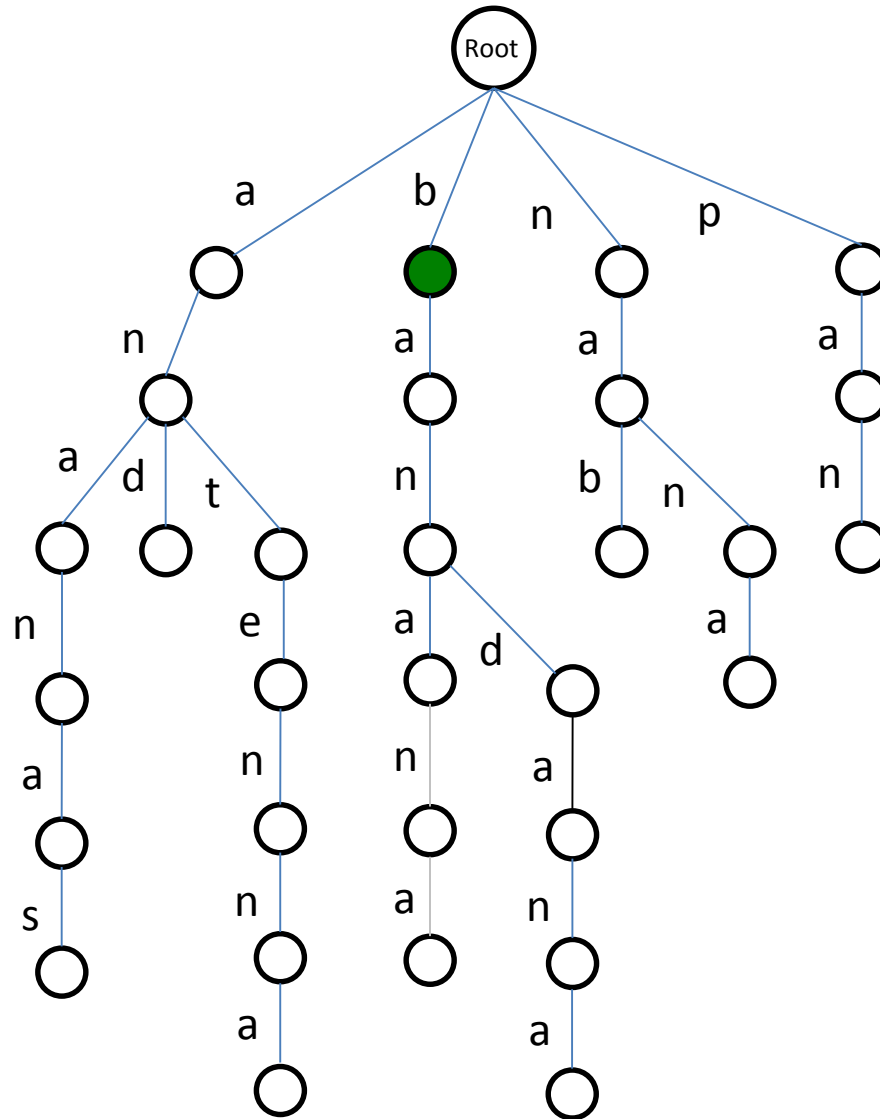
panama bananas



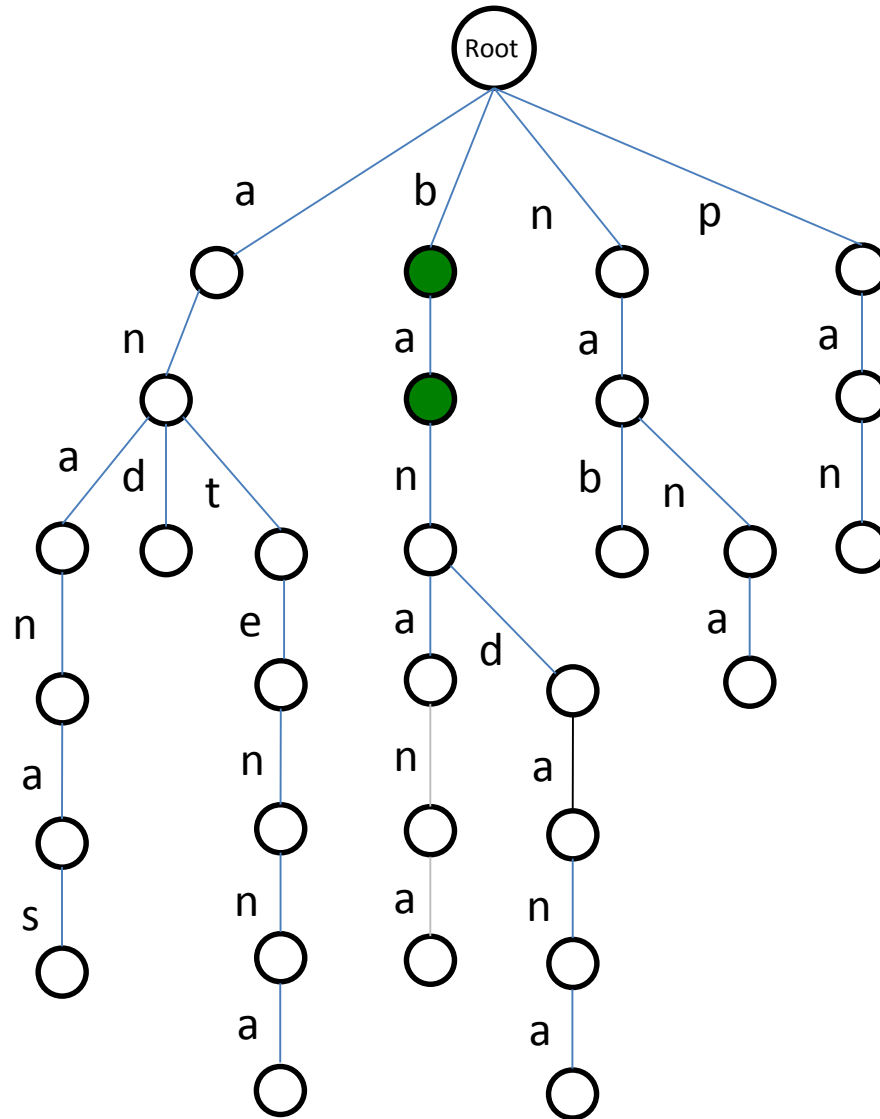
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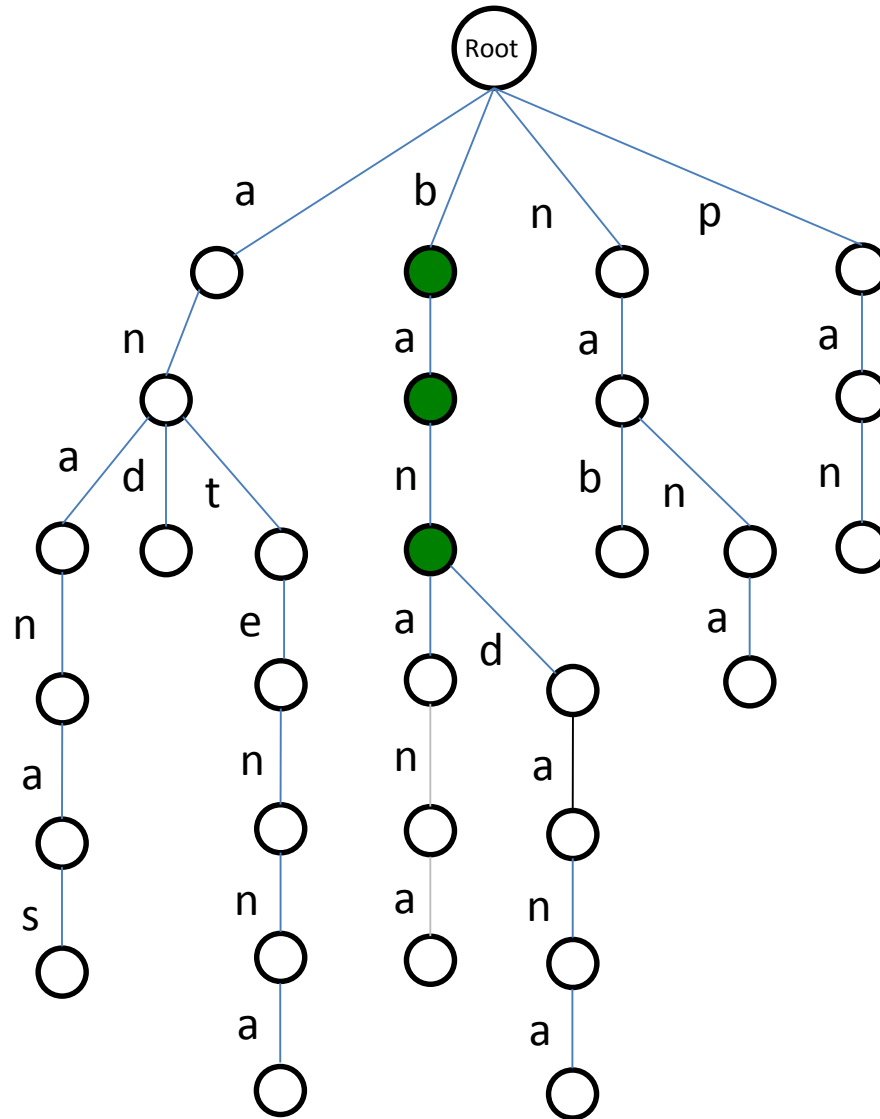
panama**b**ananas



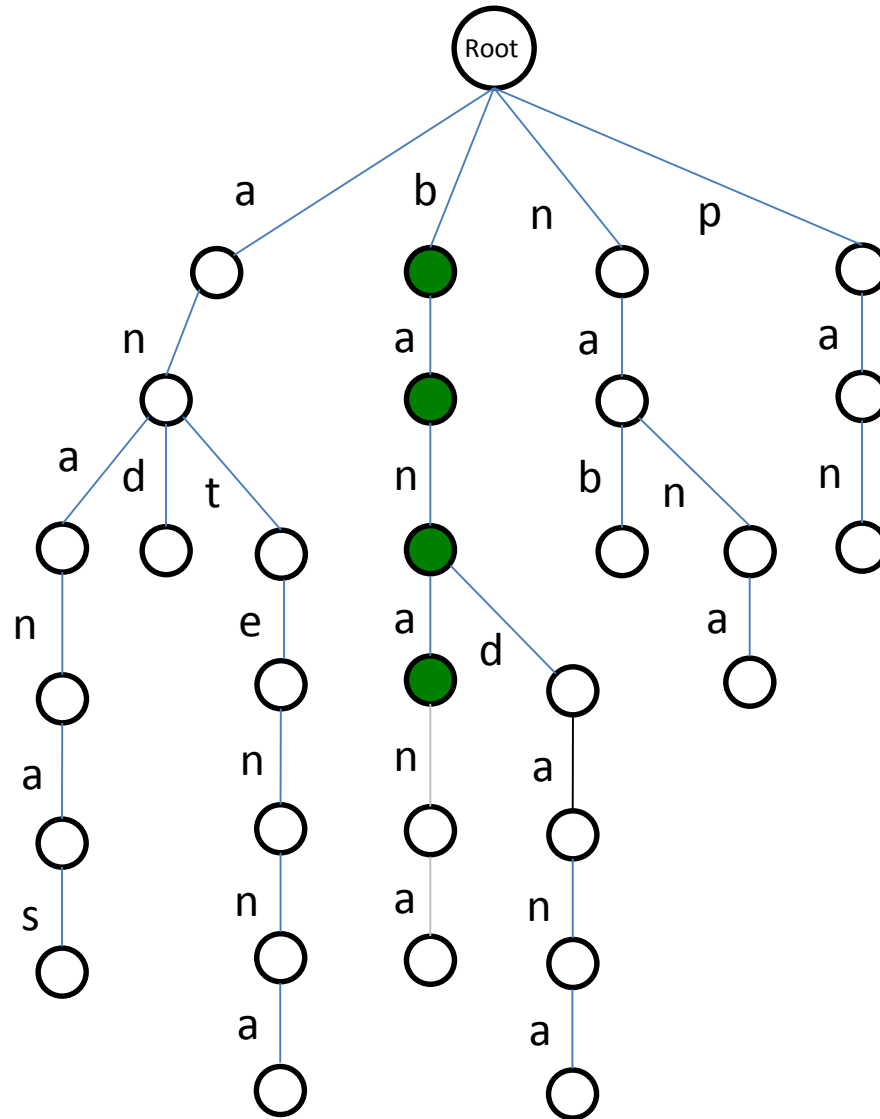
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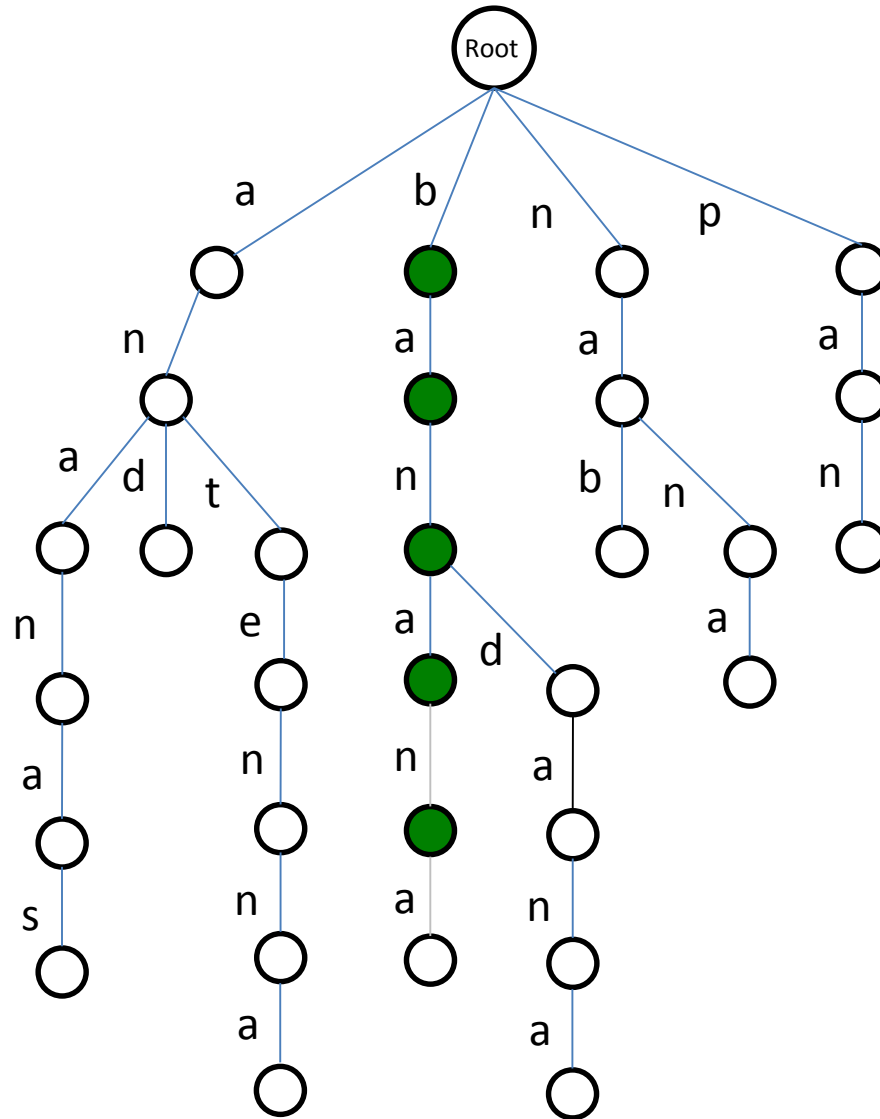
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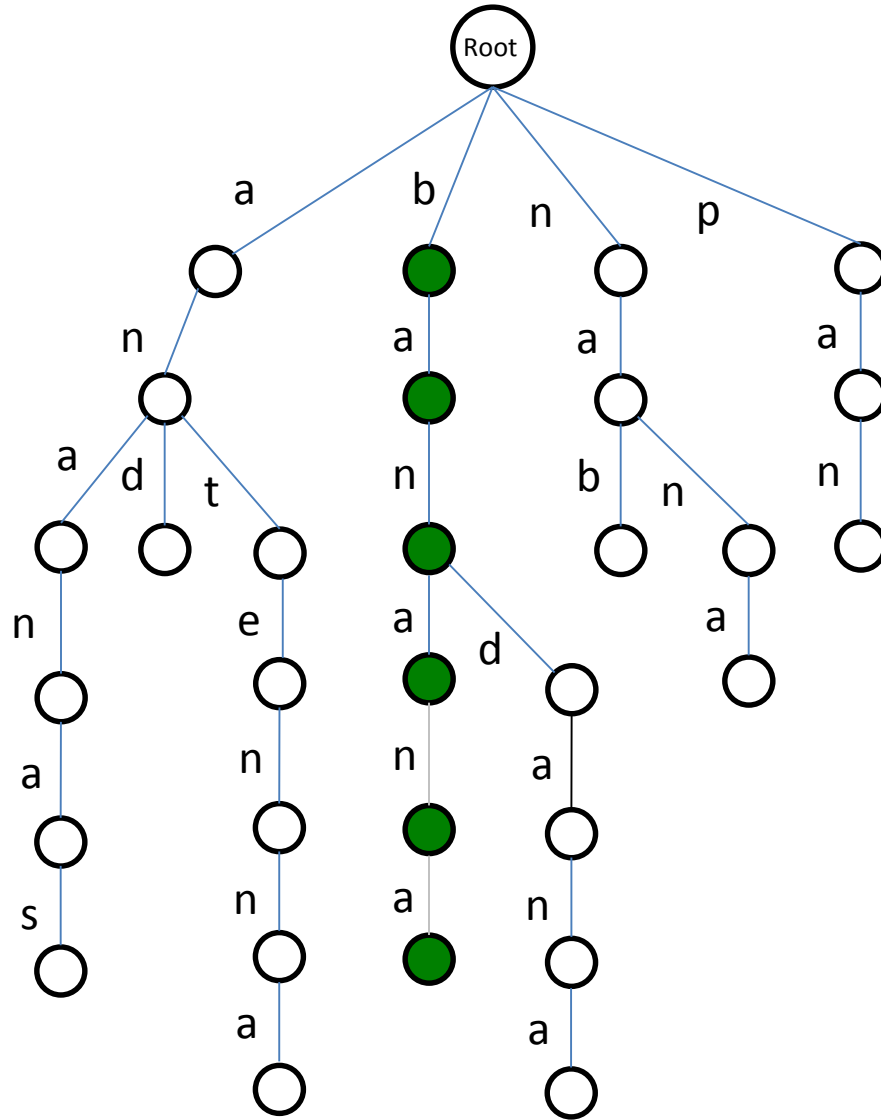
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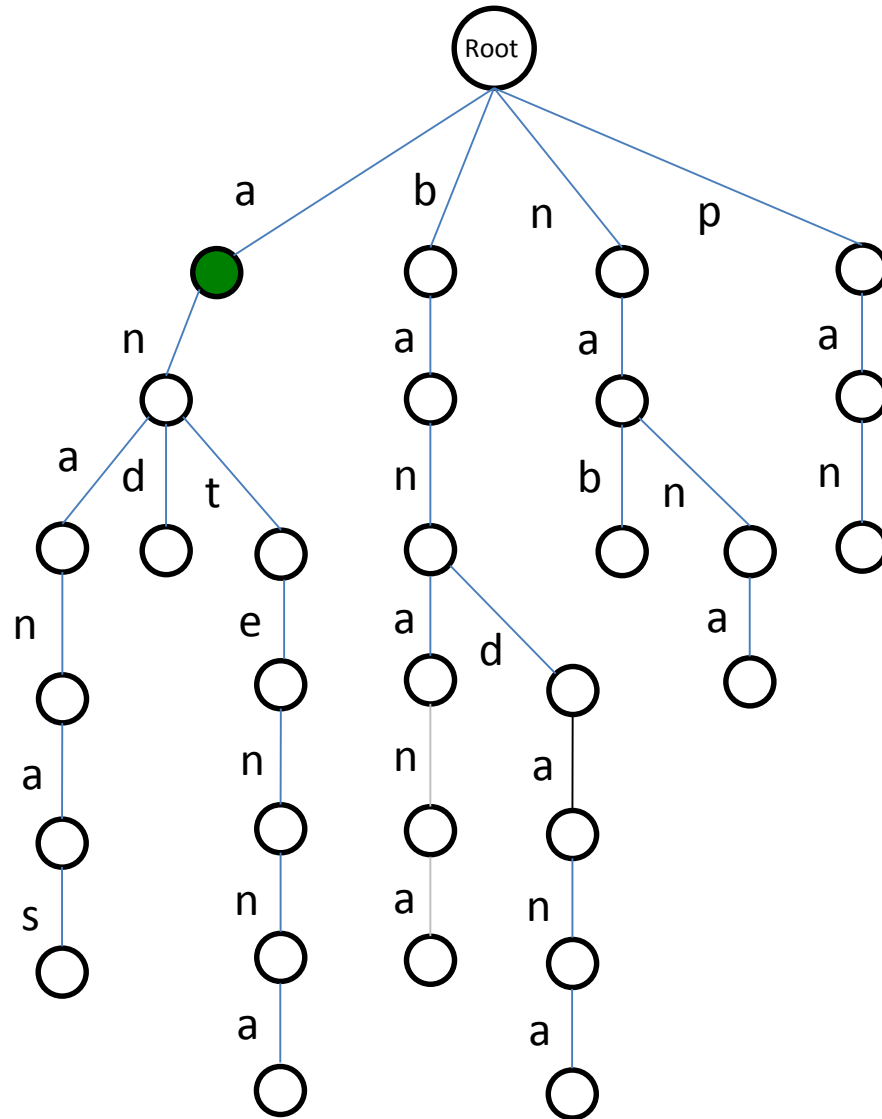
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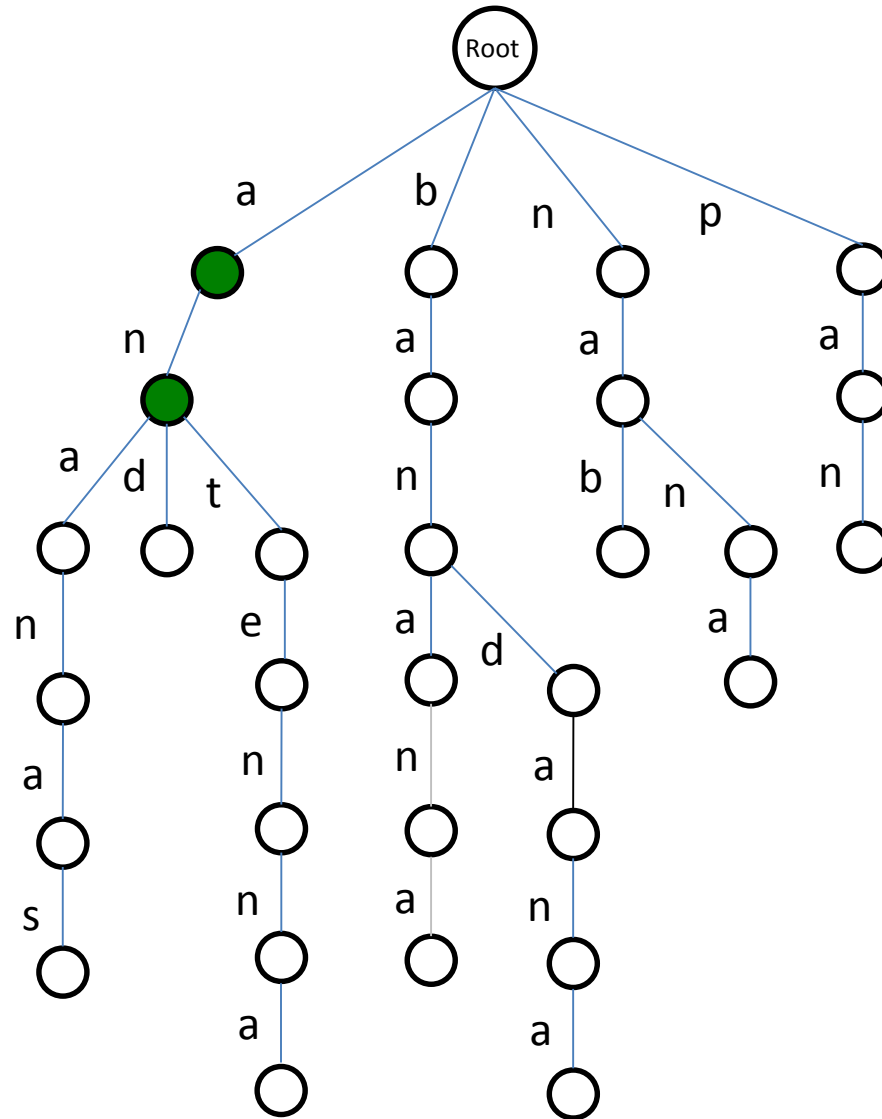
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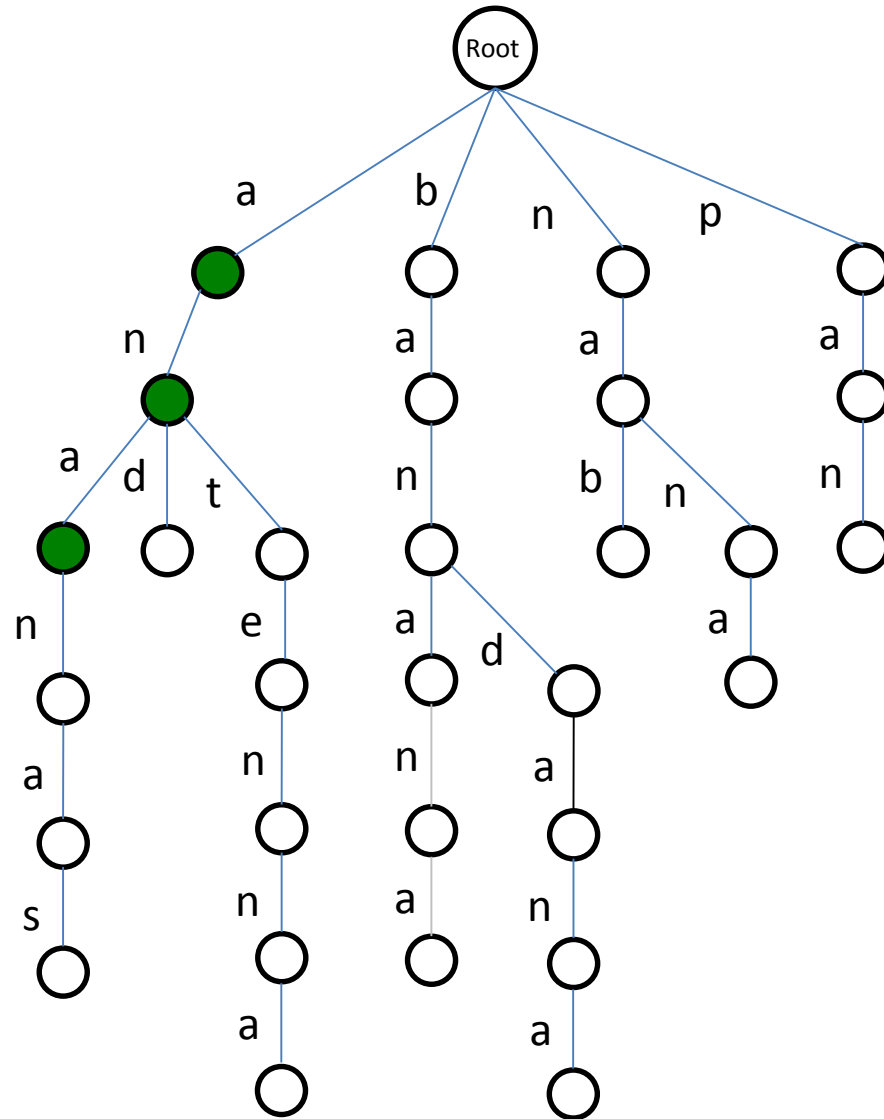
panama bananas



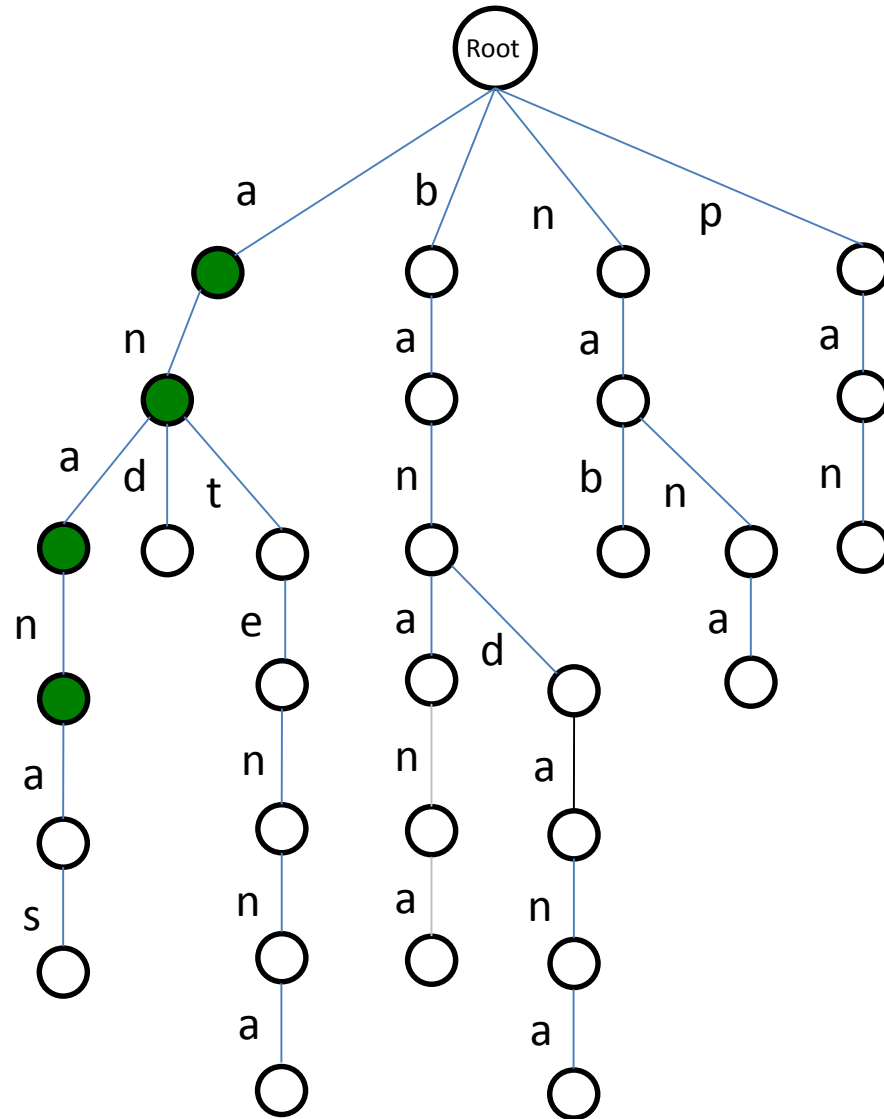
panama bananas



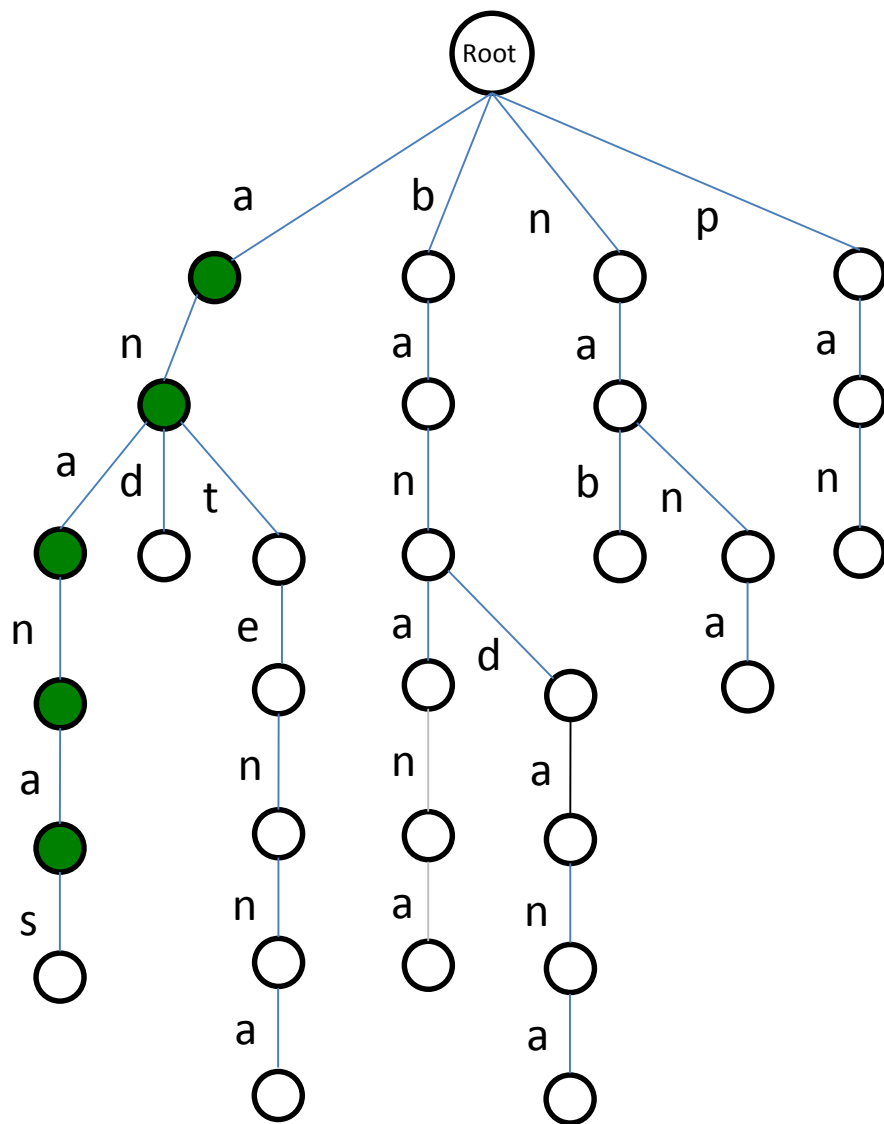
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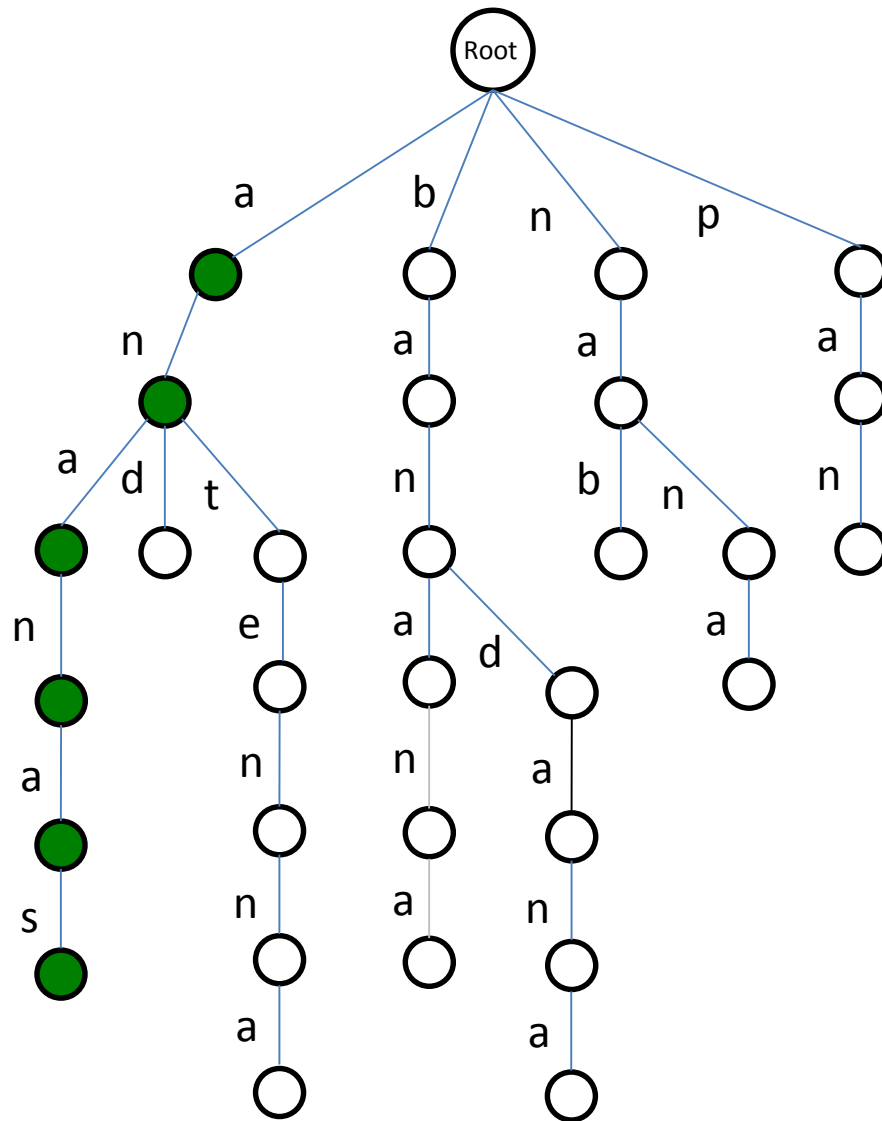
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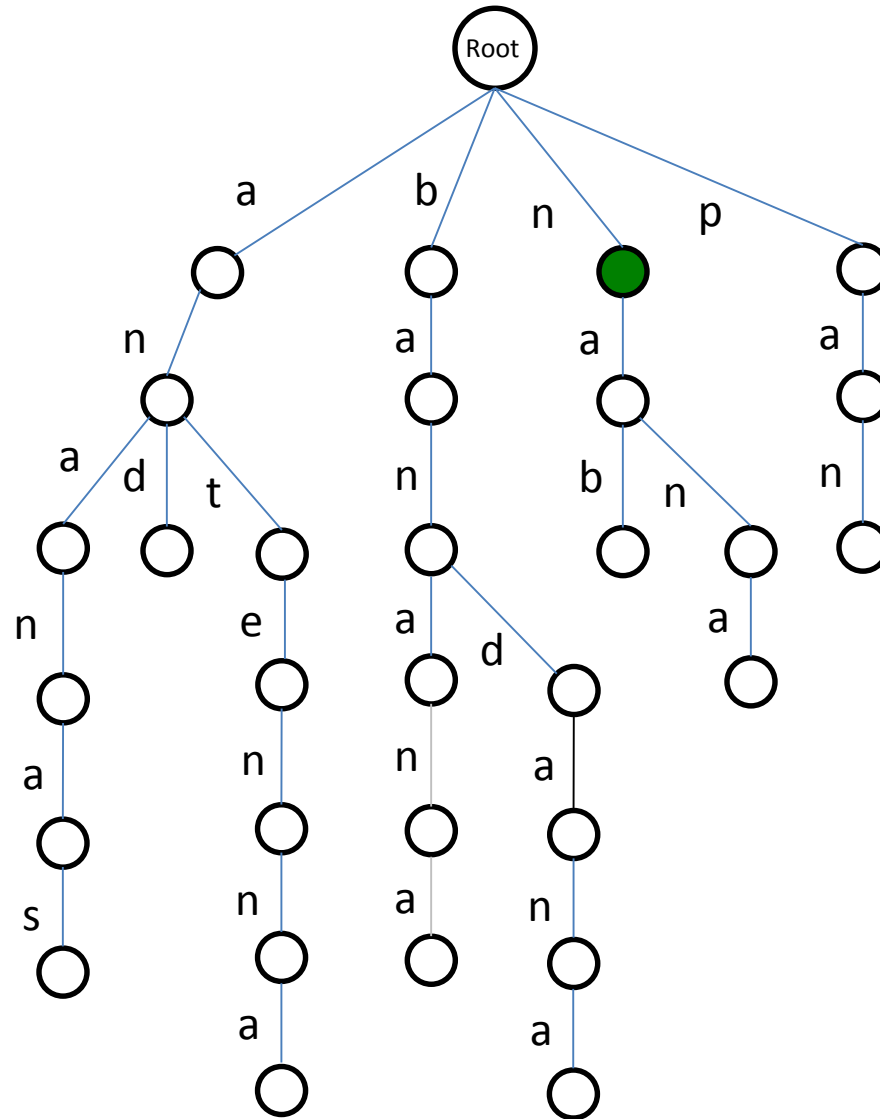
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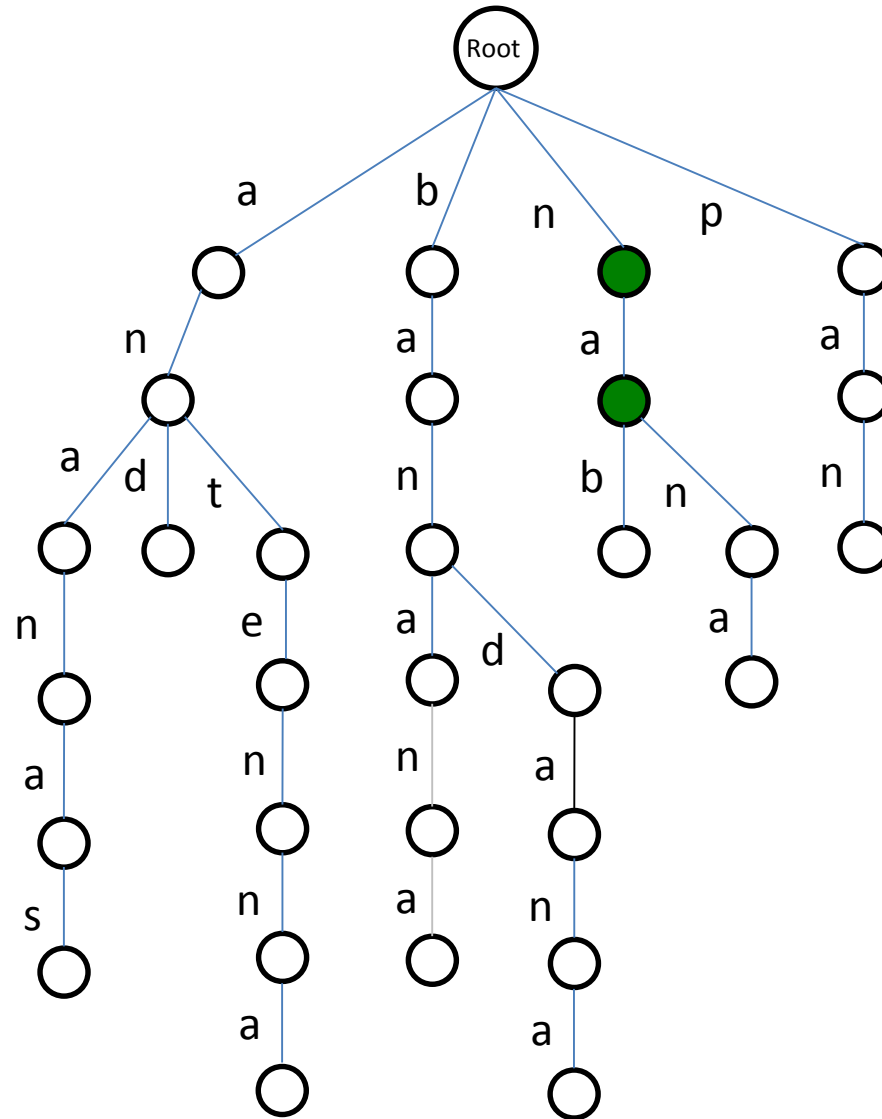
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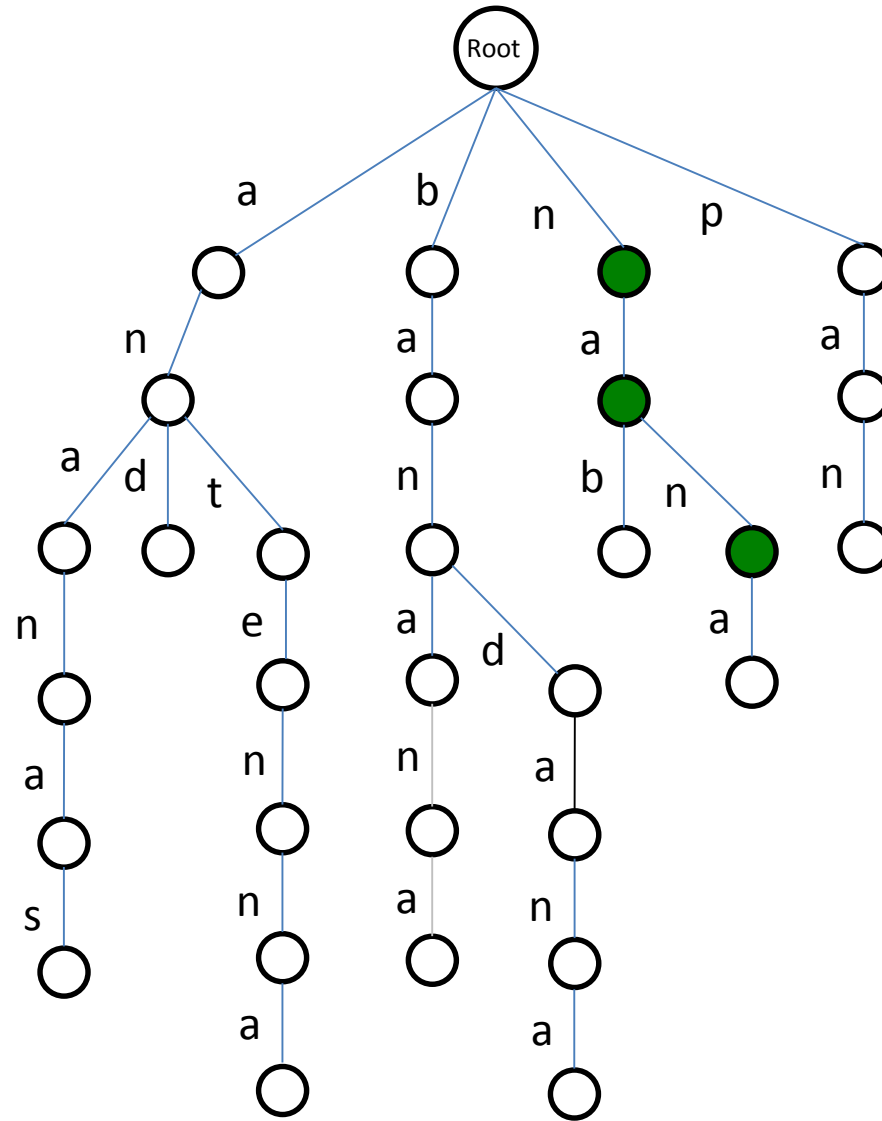
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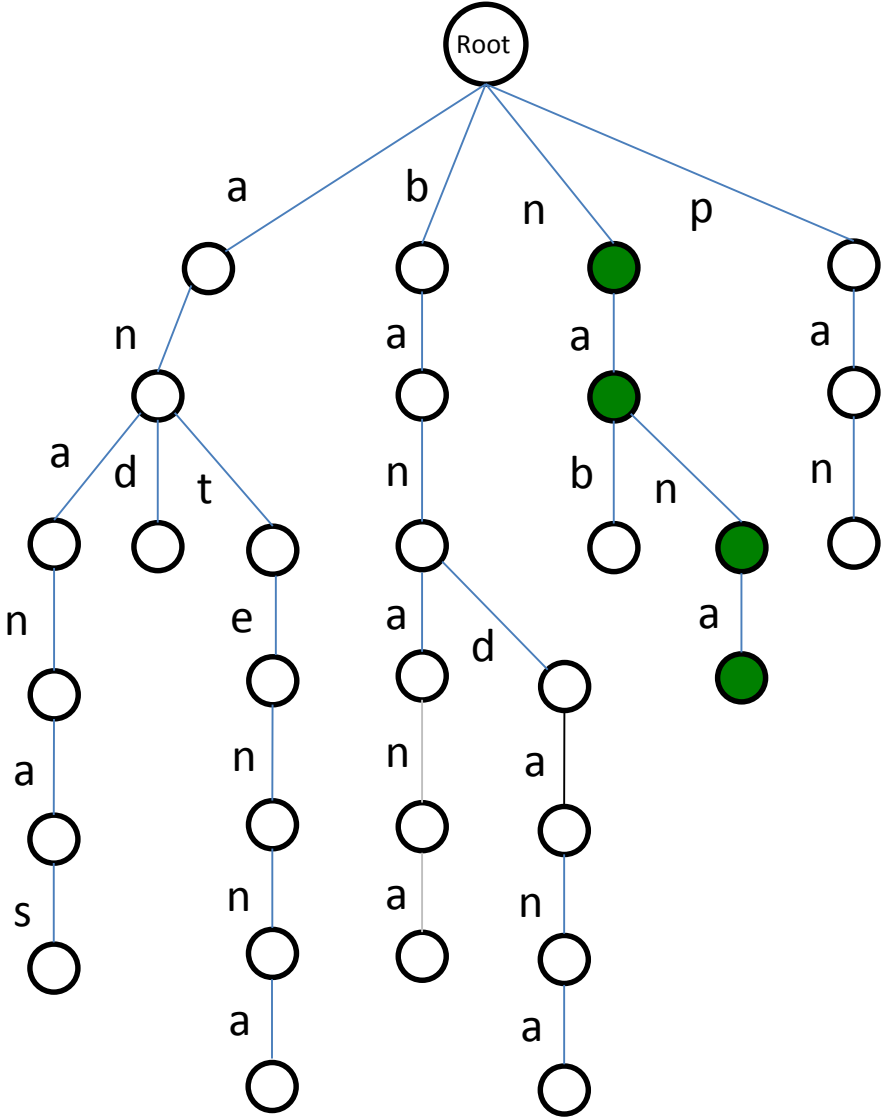
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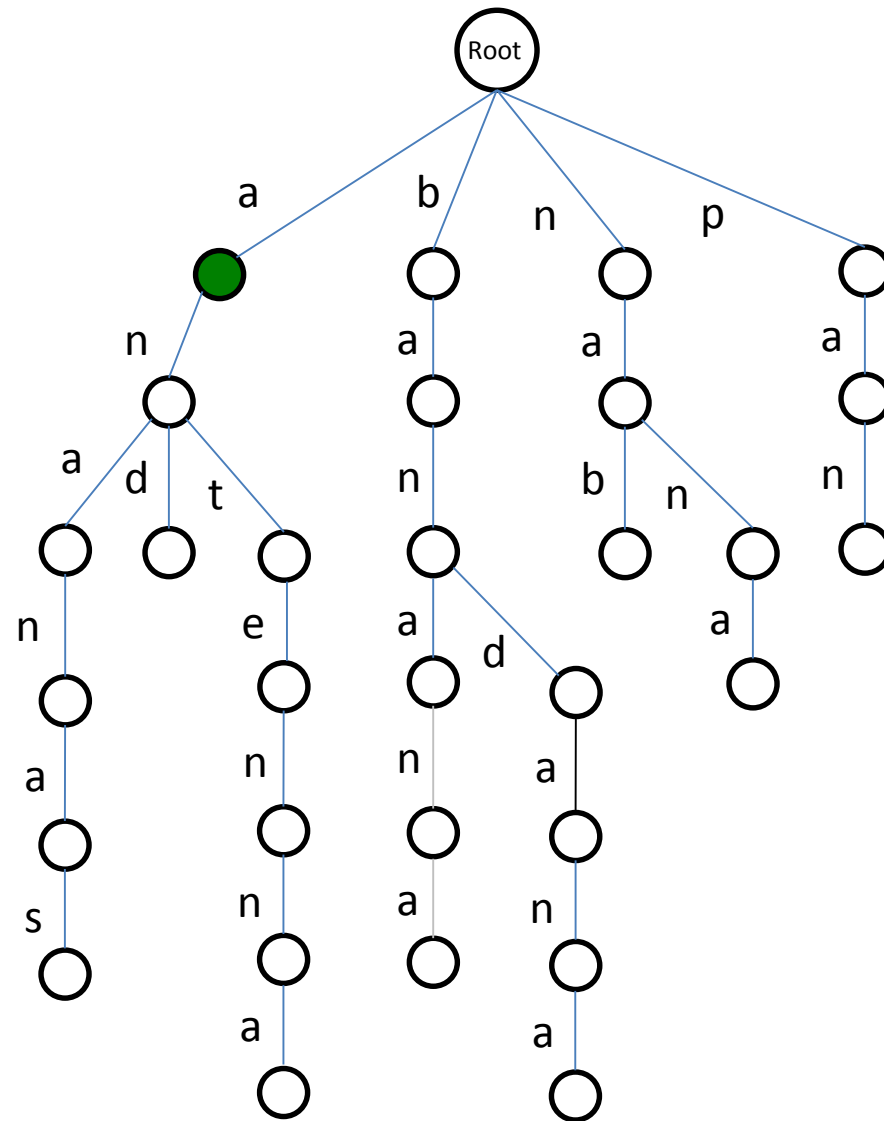
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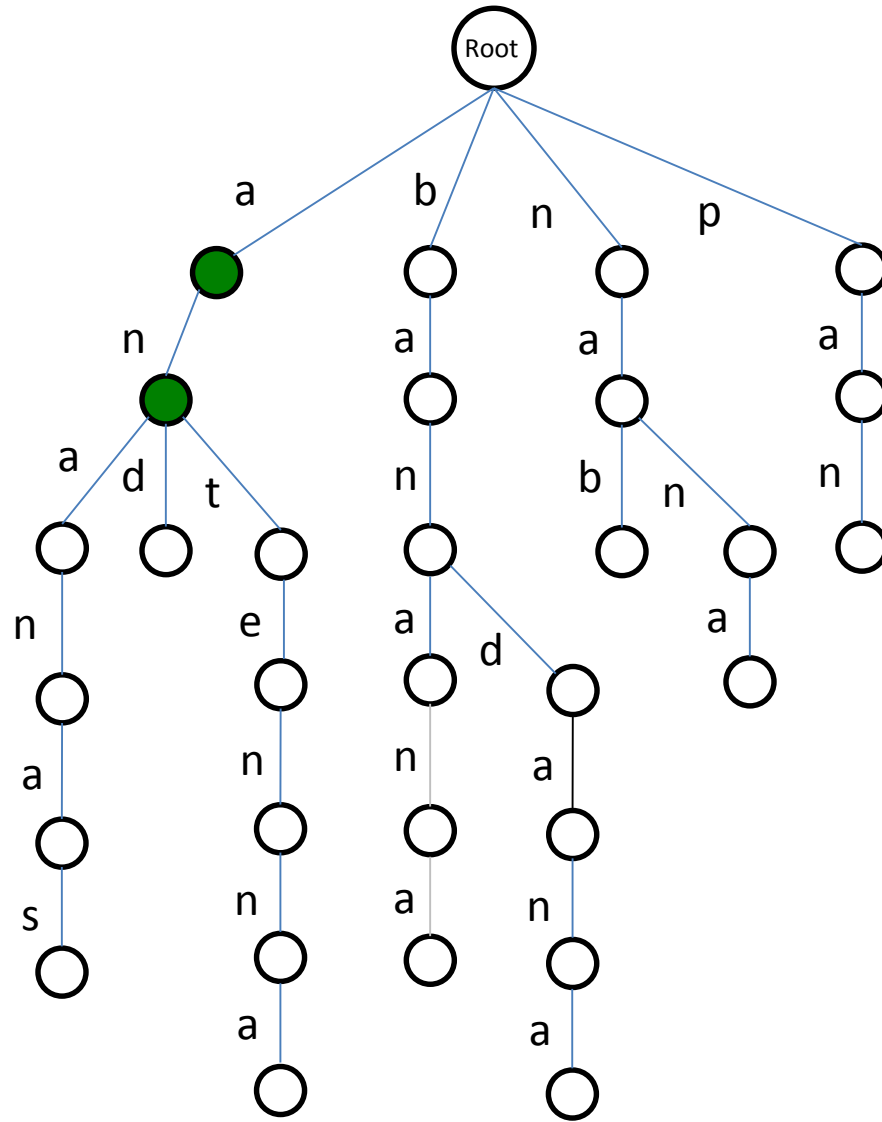
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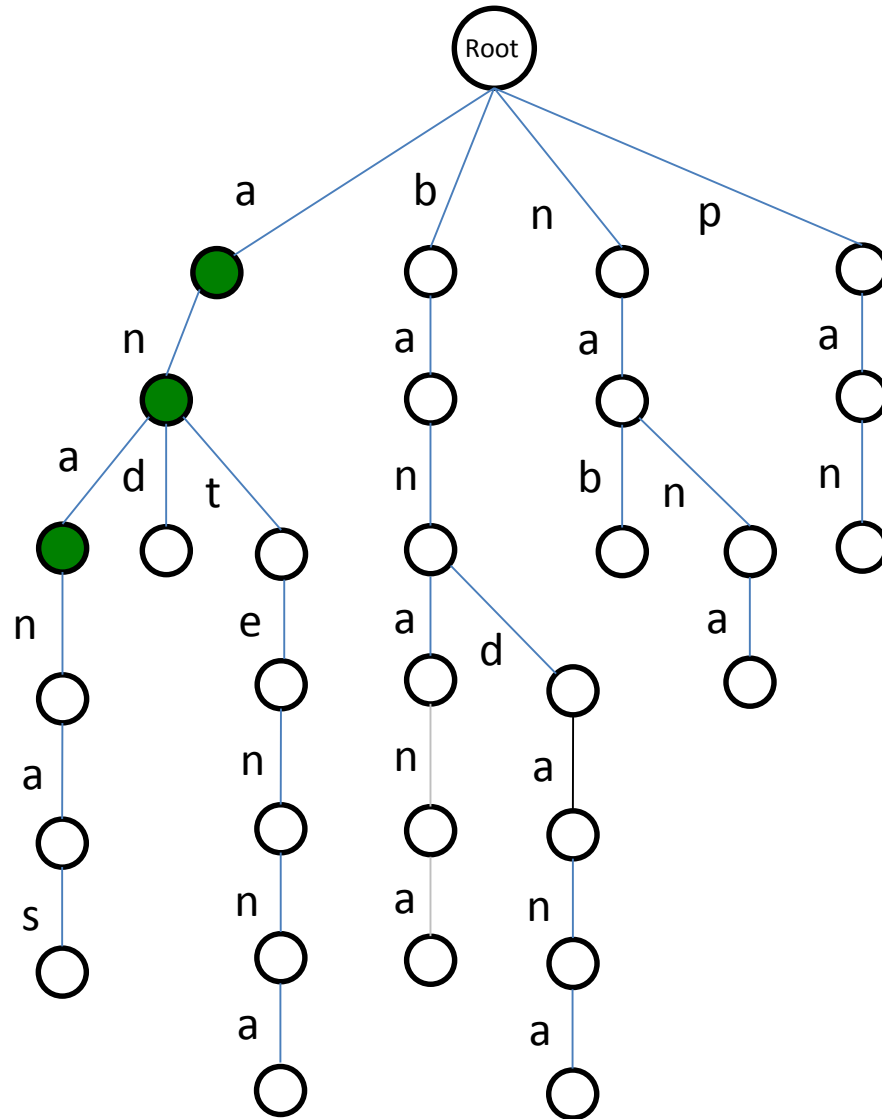
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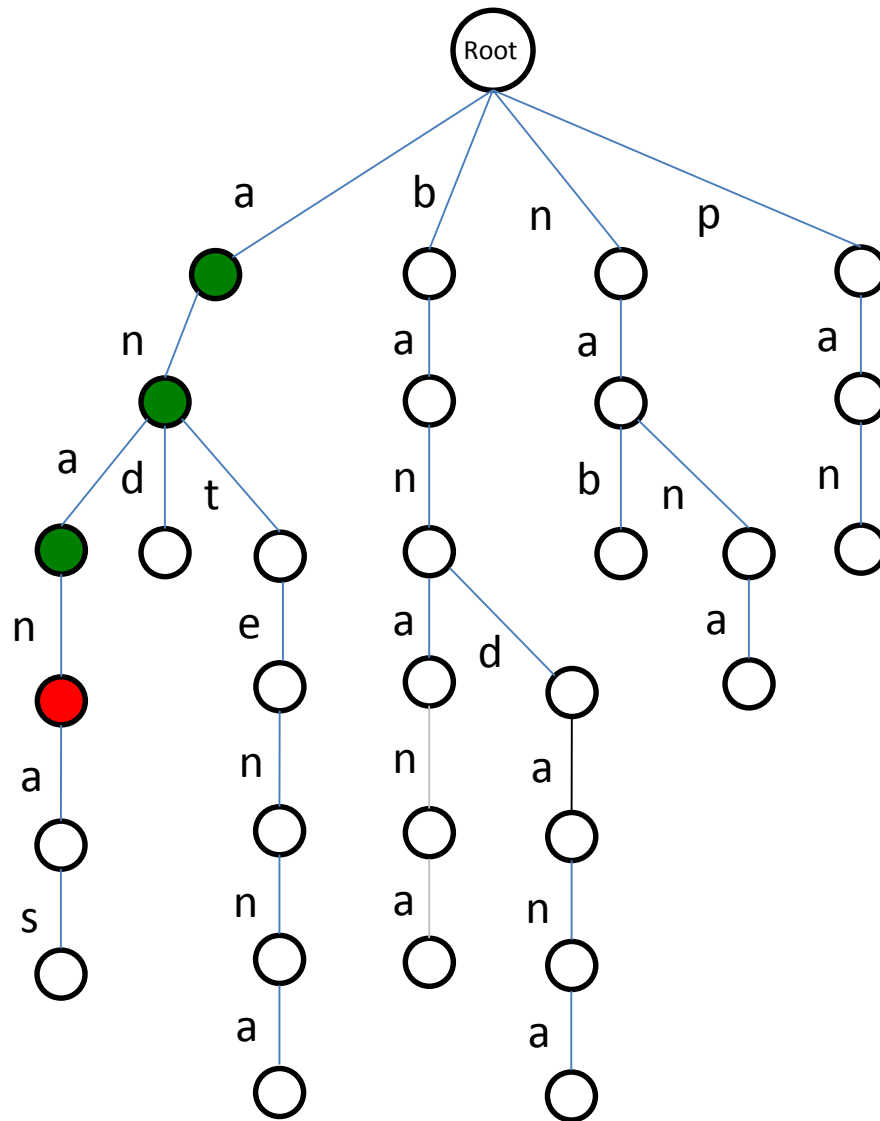
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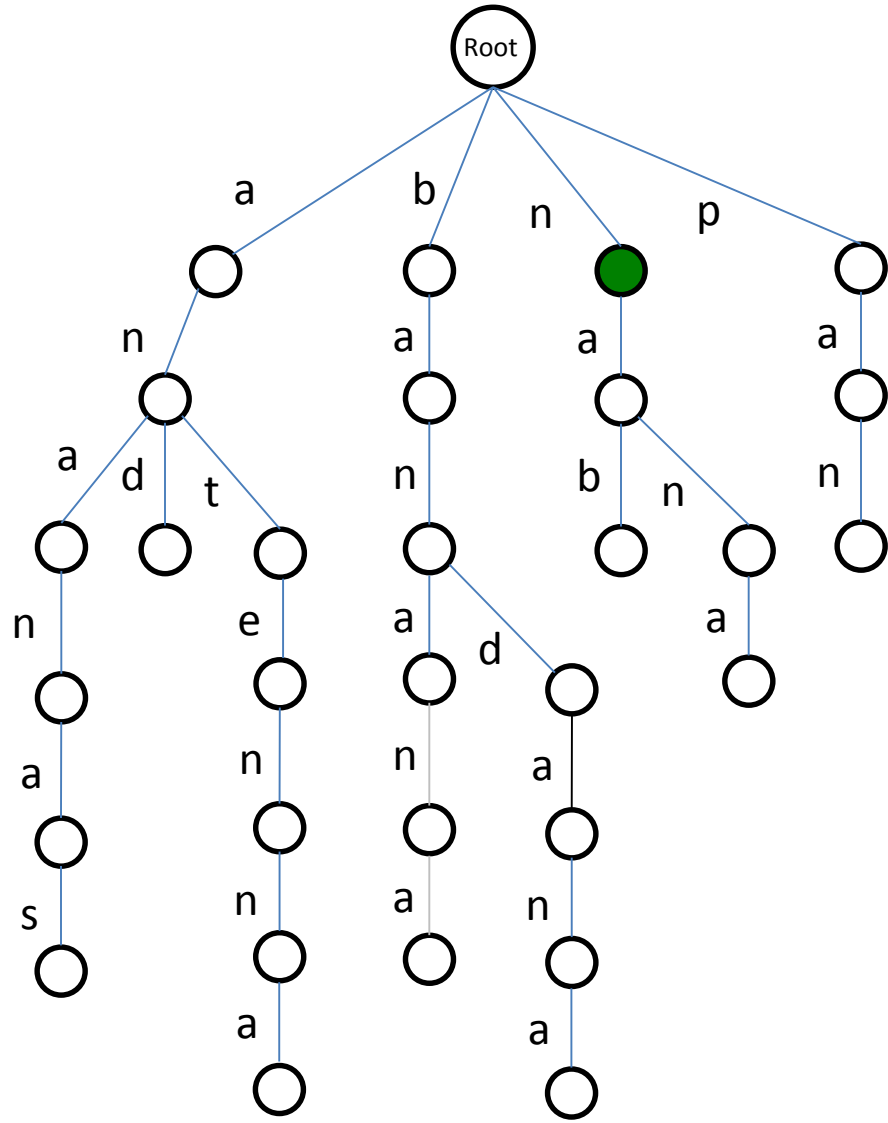
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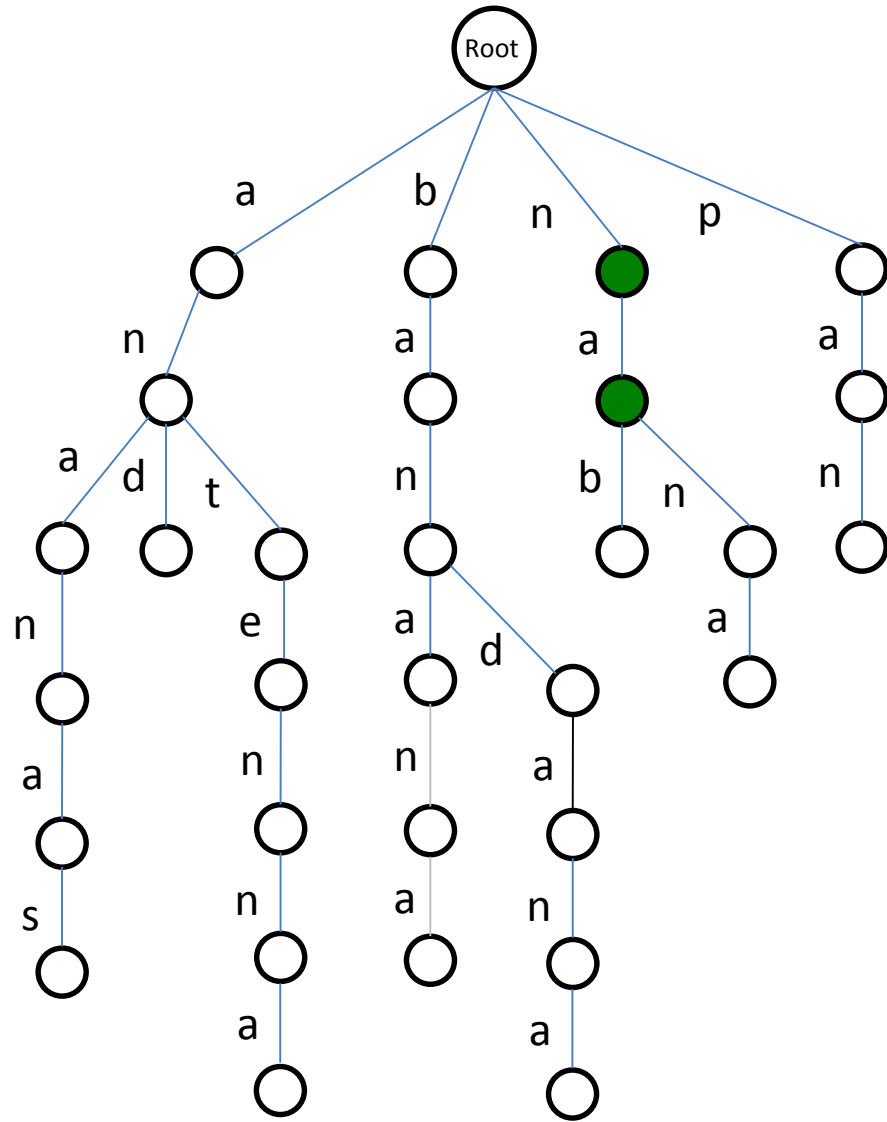
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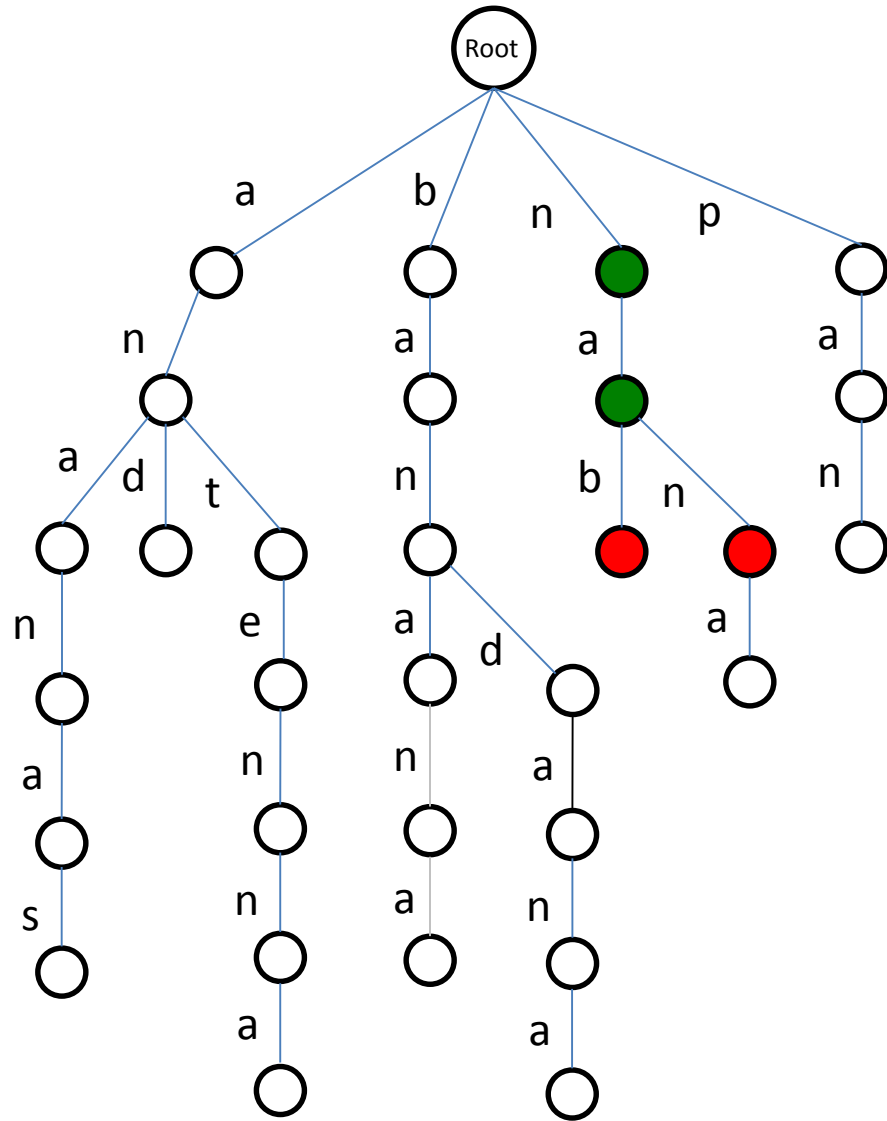
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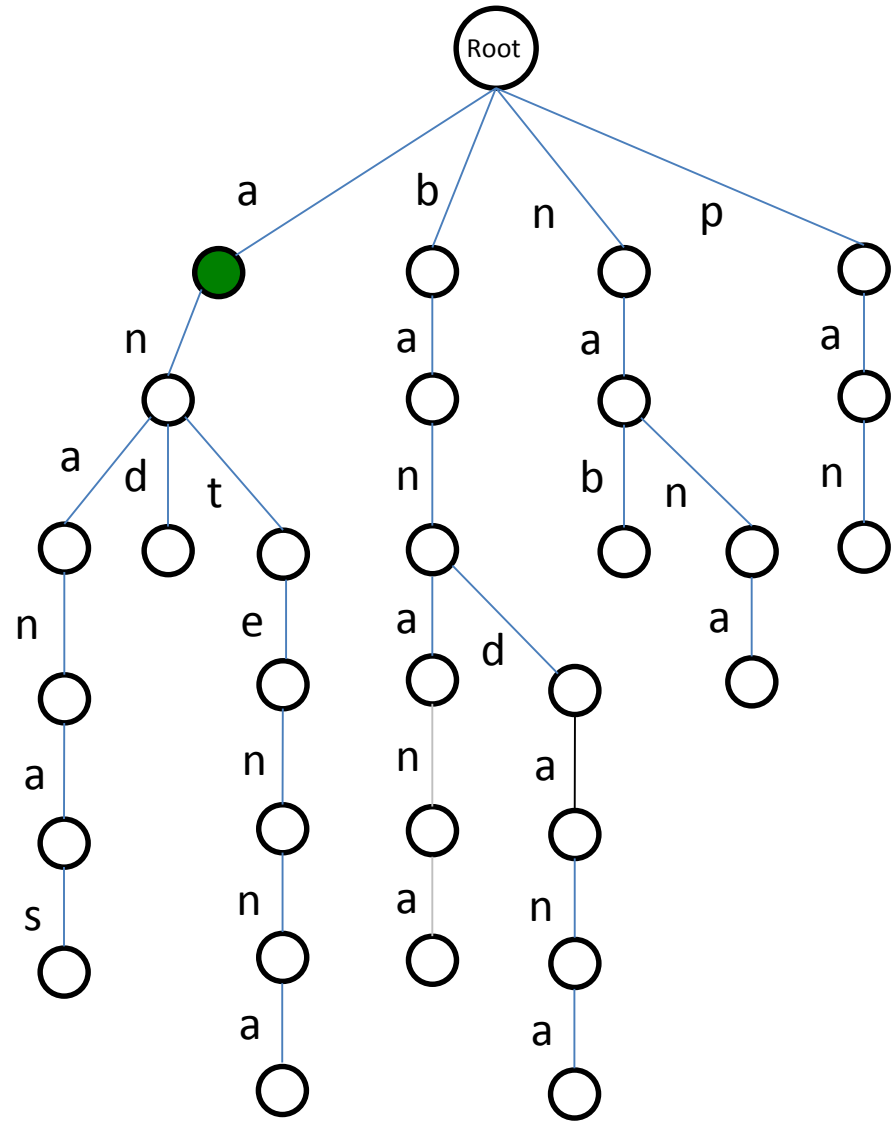
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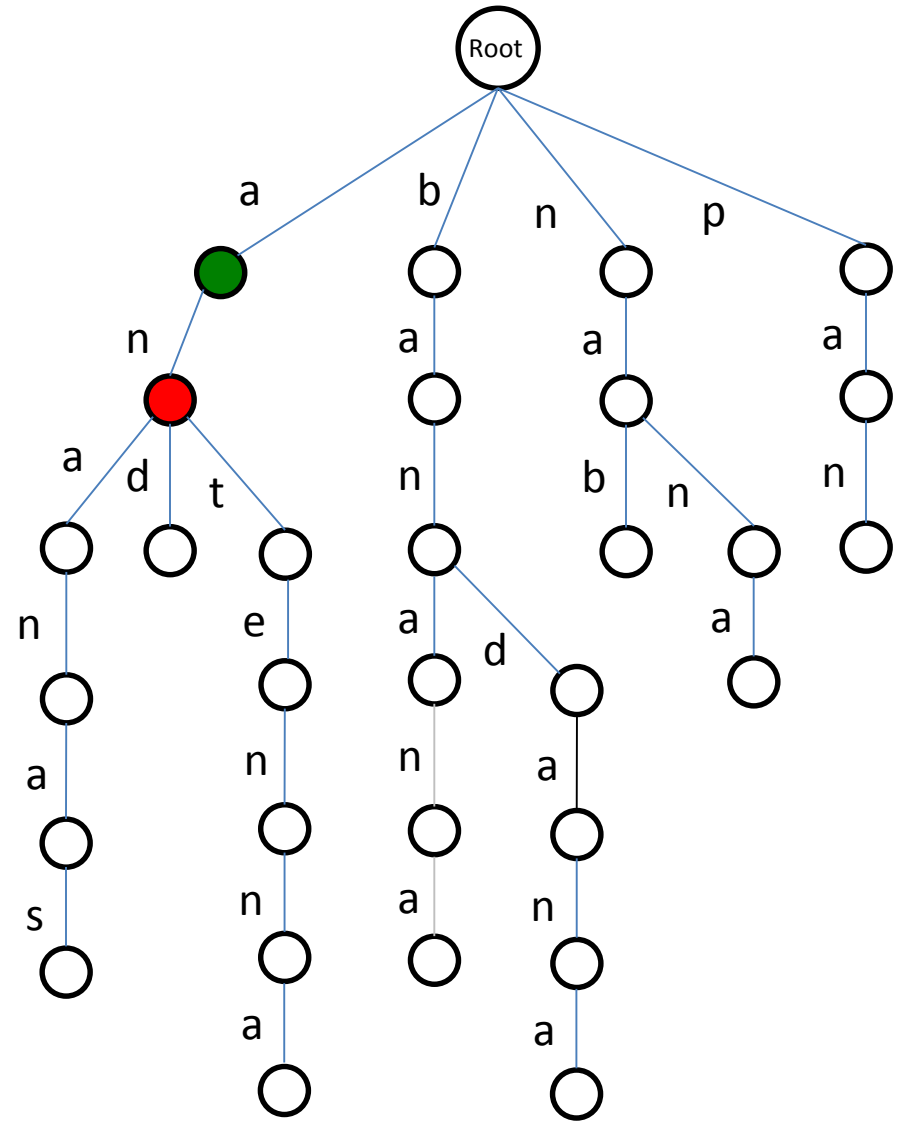
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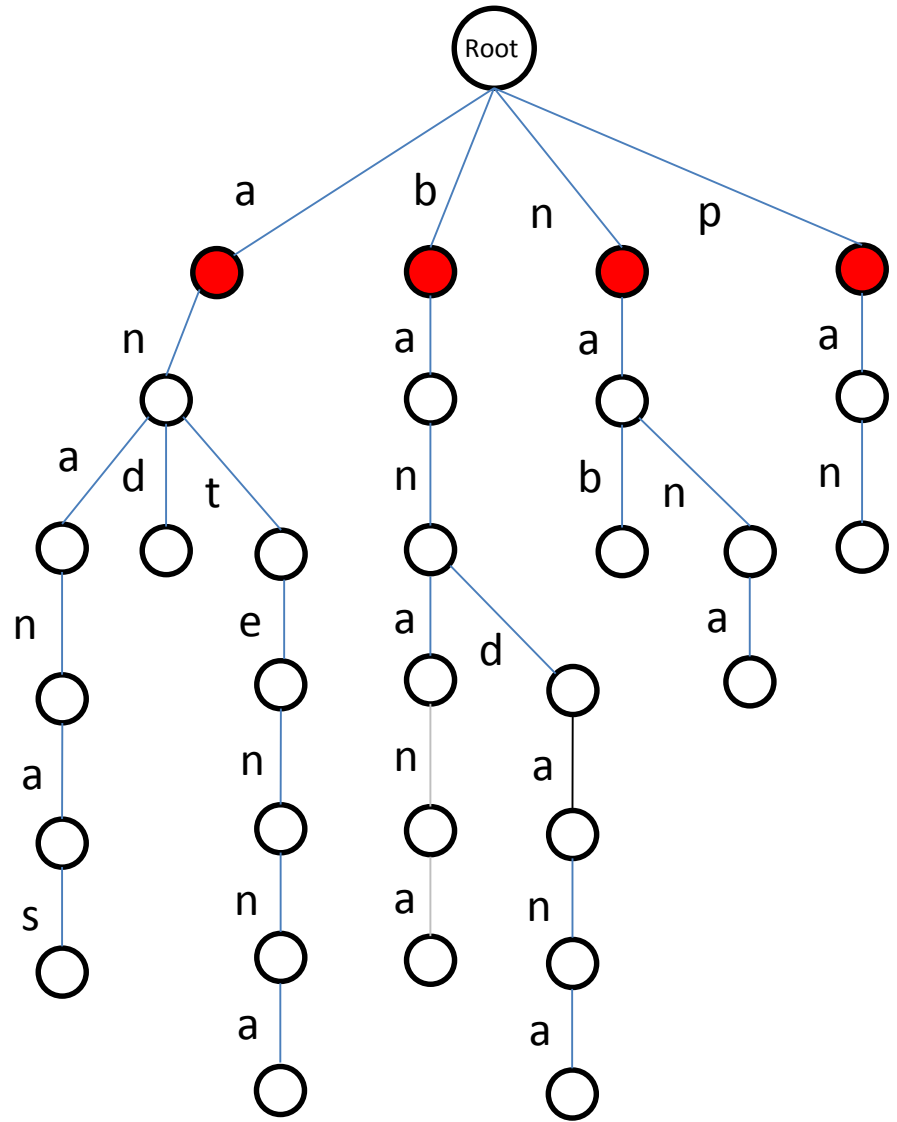
panama ban **as**



panamabanas



panama banana **s**



Our Bus Is Fast!

- Runtime of brute force approach:
 - $O(|Text| \cdot |Patterns|)$
- Runtime of **TrieMatching**:
 - $O(|Text| * |LongestPattern|)$

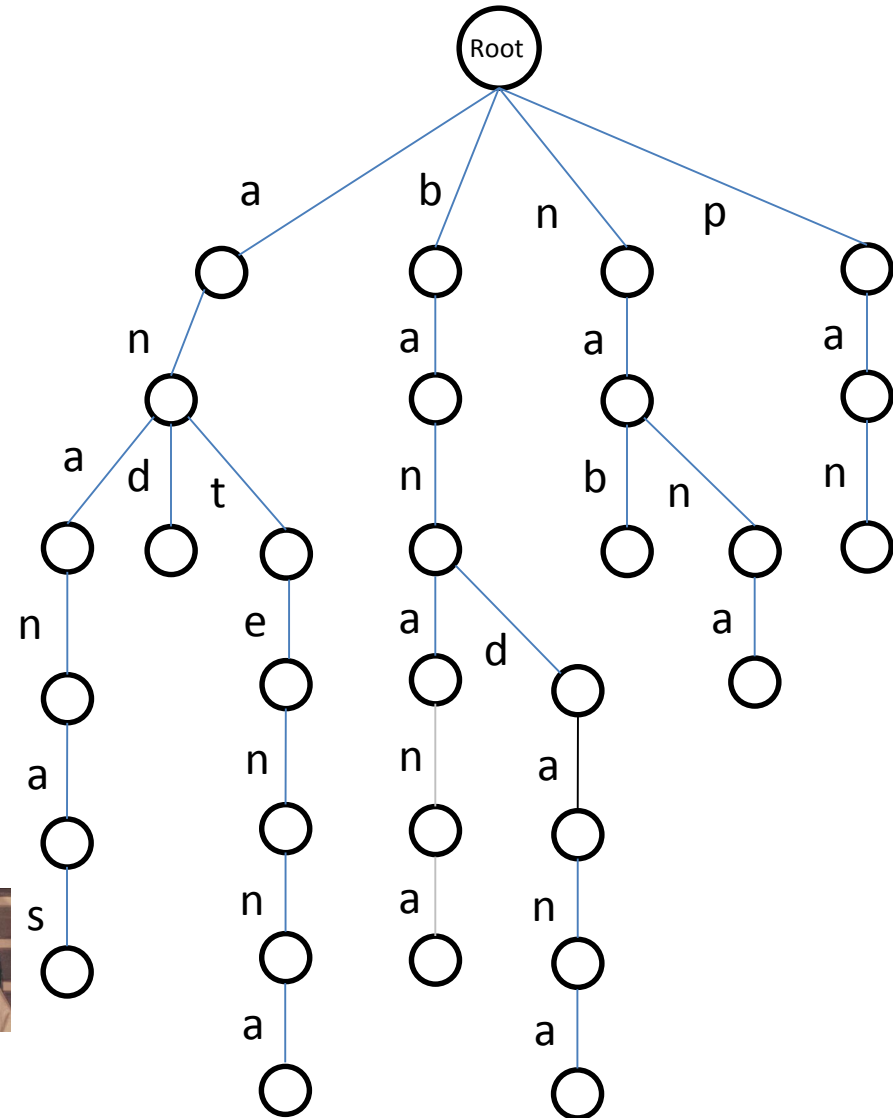


Trie construction takes $O(|Patterns|)$ time

Memory Footprint of TrieMatching

- Our trie has 30 edges
- # edges = $O(|Patterns|)$!

- For human genome:
 $|Patterns| \approx 10^{12}$



Outline

- From Genome Sequencing to Pattern Matching
- Brute Force Approach to Pattern Matching
- Herding Patterns into Trie
- **Herding Text into Suffix Trie**
- From Suffix Tries to Suffix Trees

New Idea: Packing *Text* onto a Bus

- Generate all suffixes of *Text*
- Form a trie out of these suffixes (**suffix trie**)
- For each *Pattern*, check if it can be spelled out from the root downward in the suffix trie

Root

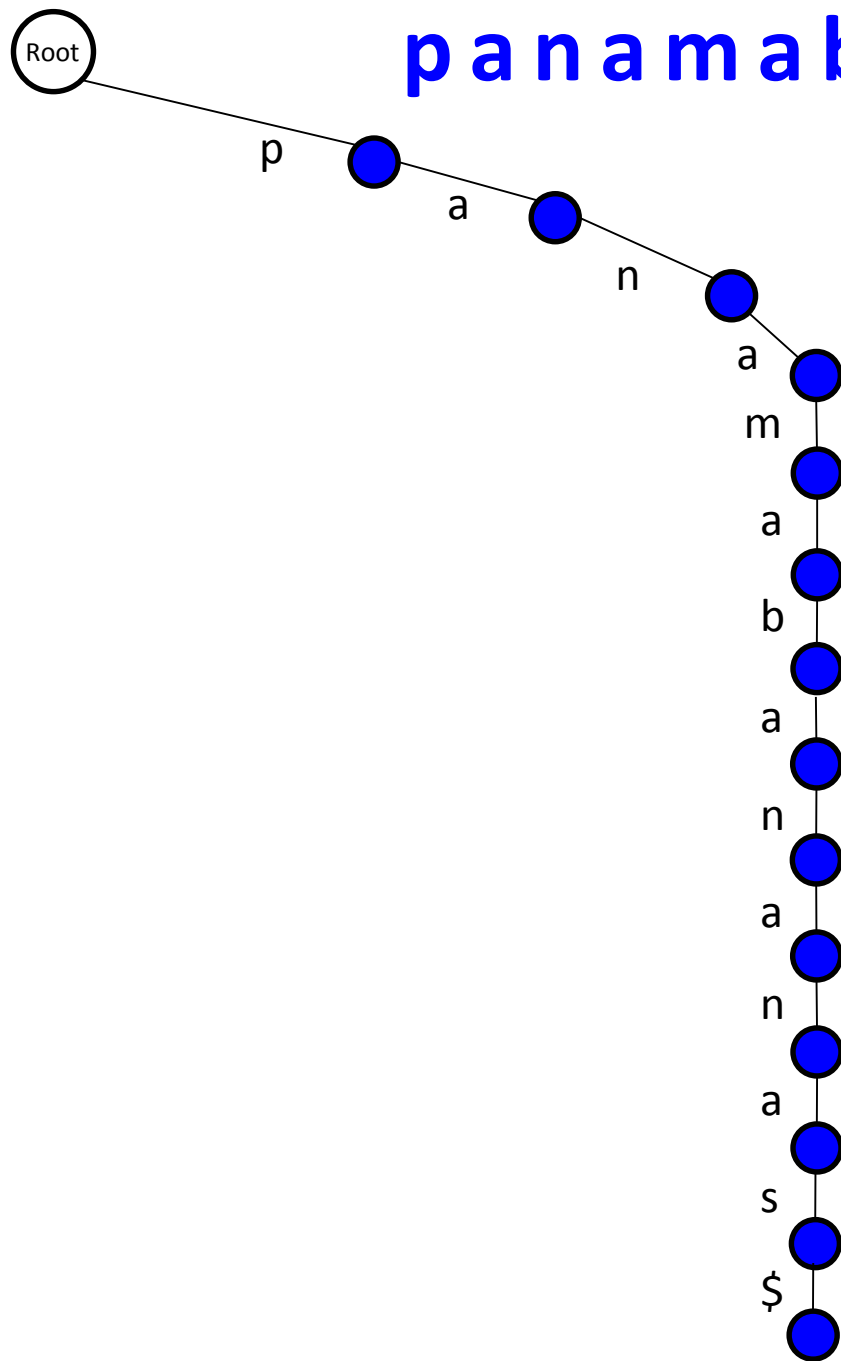
p a n a m a b a n a n a s



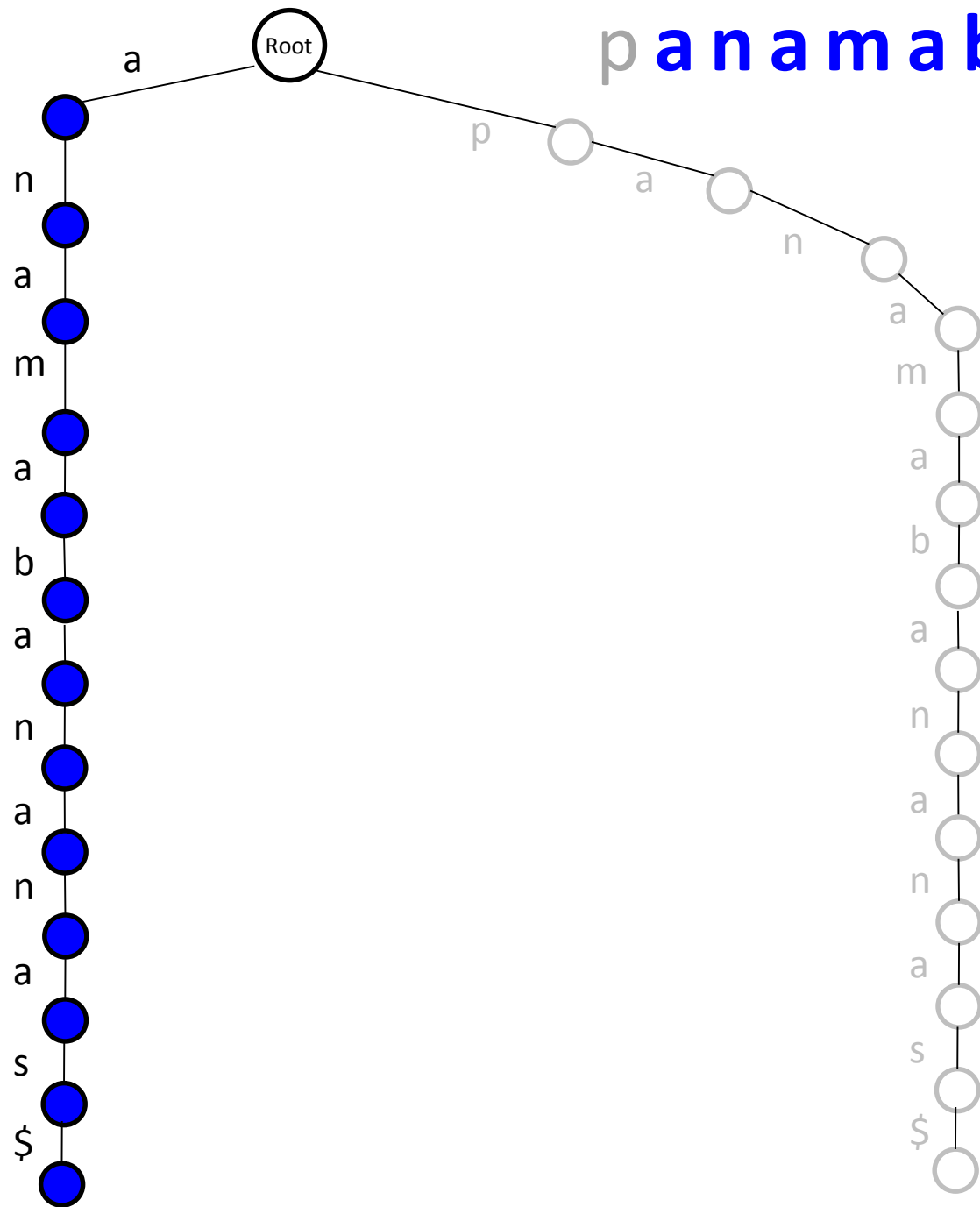
p a n a m a b a n a n a s \$

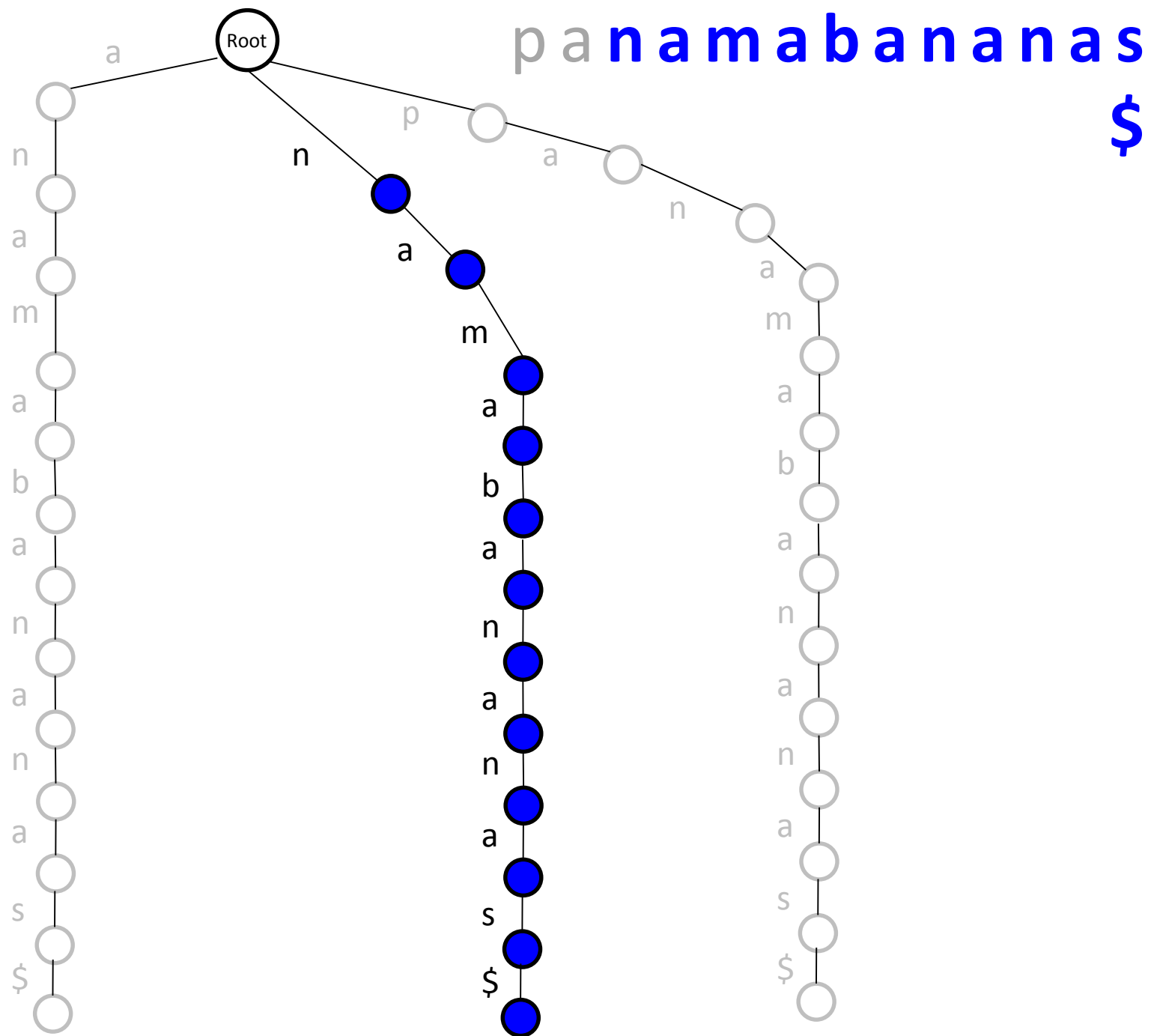
Adding “\$” sign in the end (we’ll explain later why)

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\$

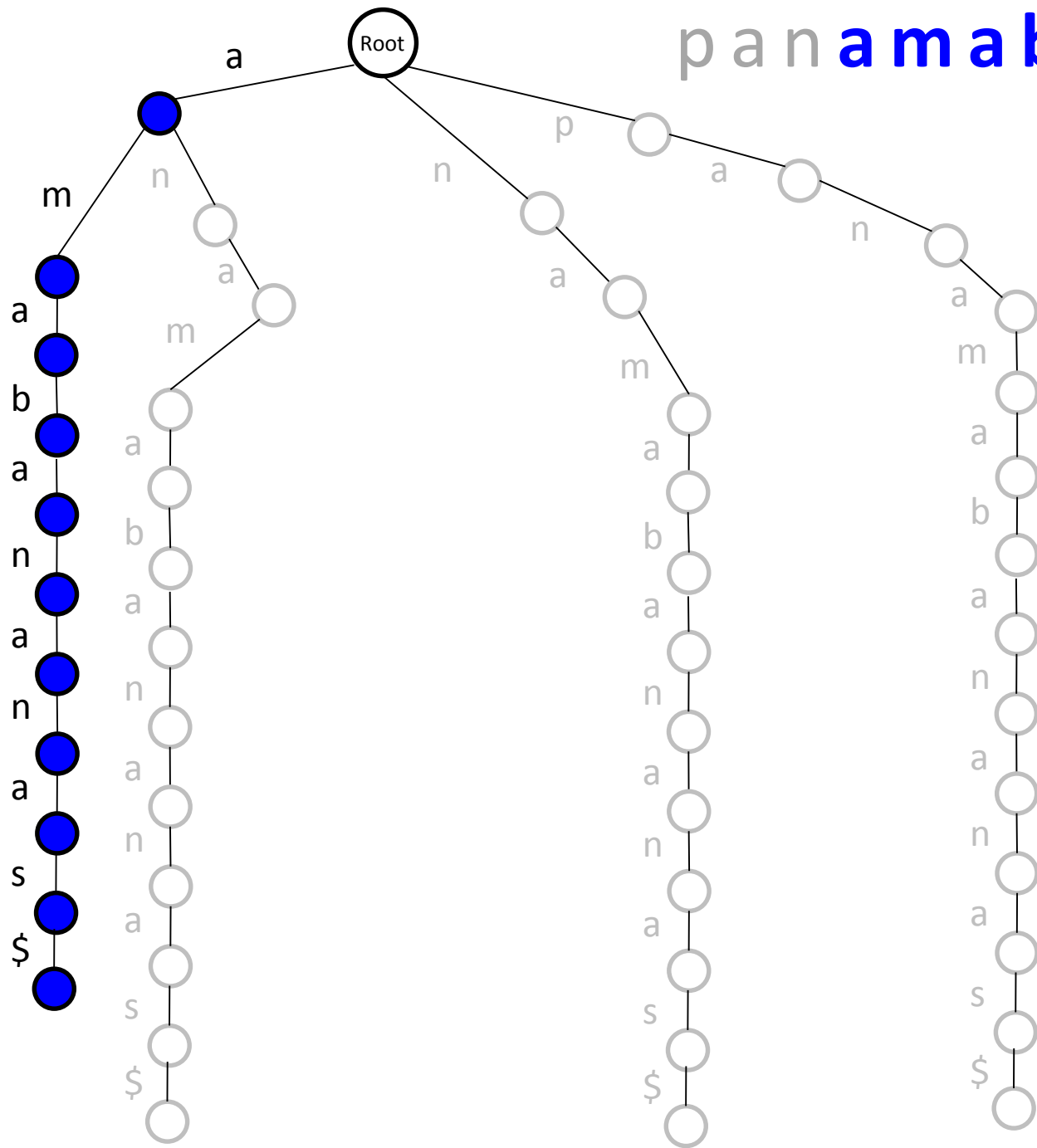


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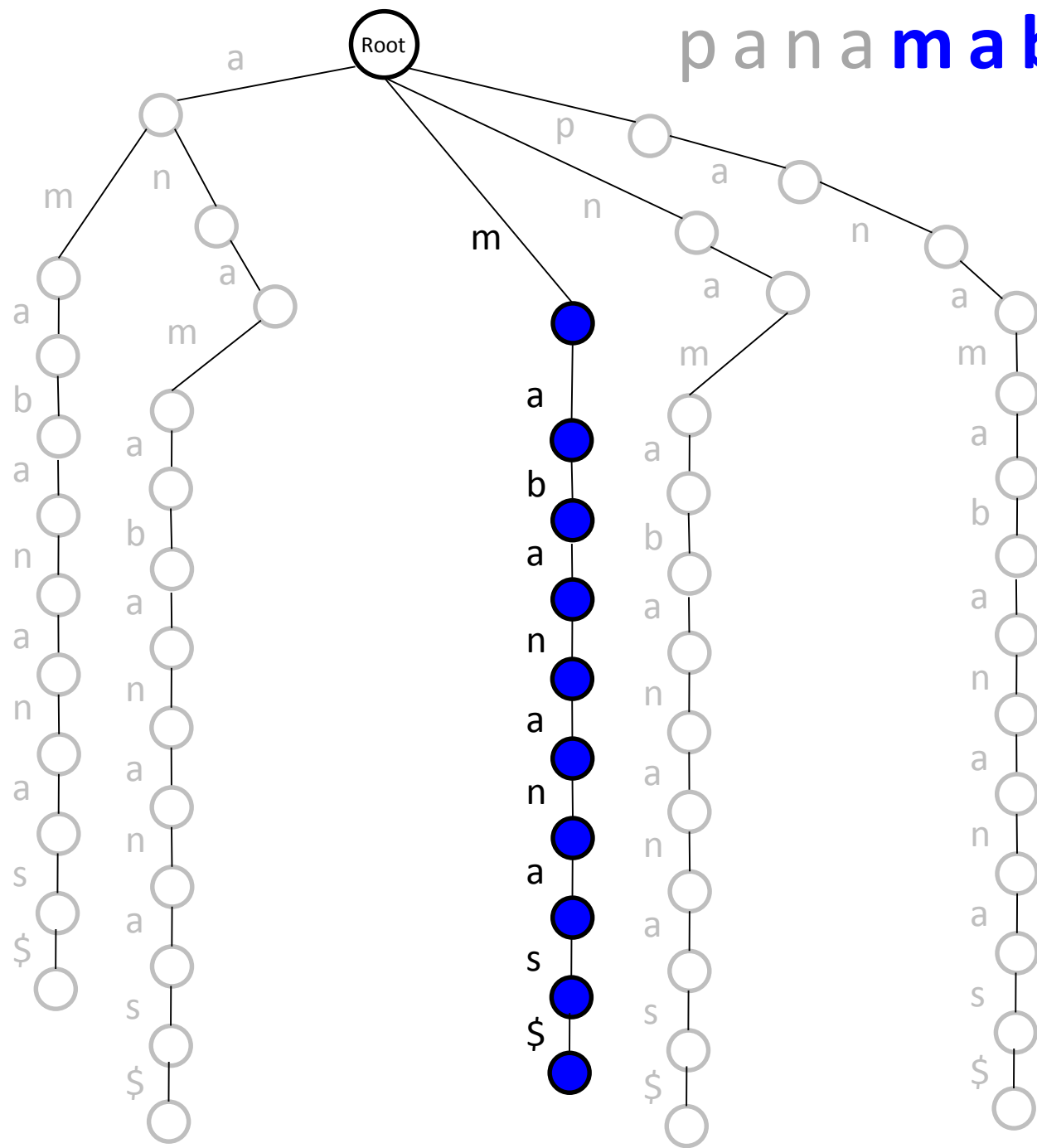




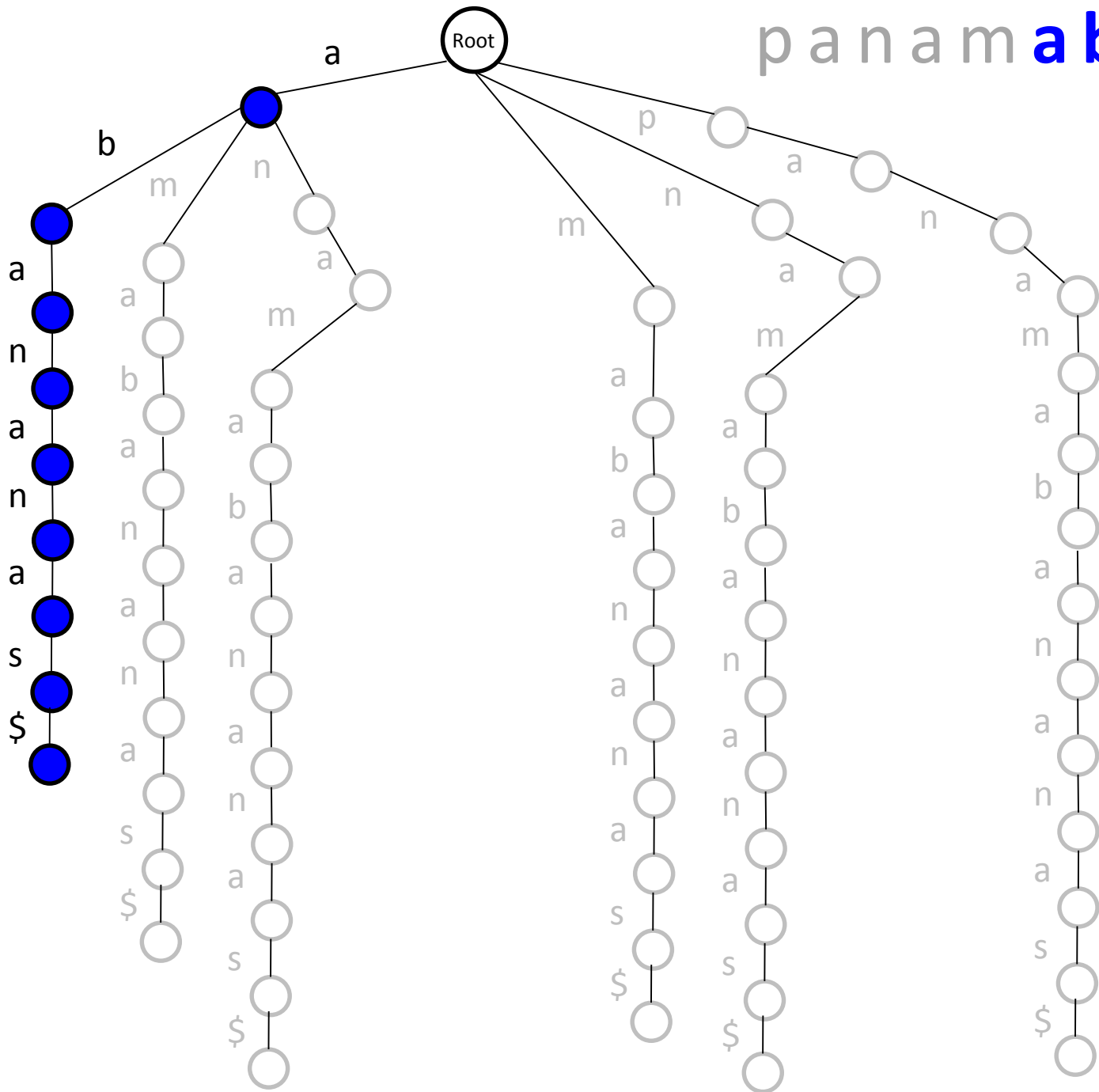
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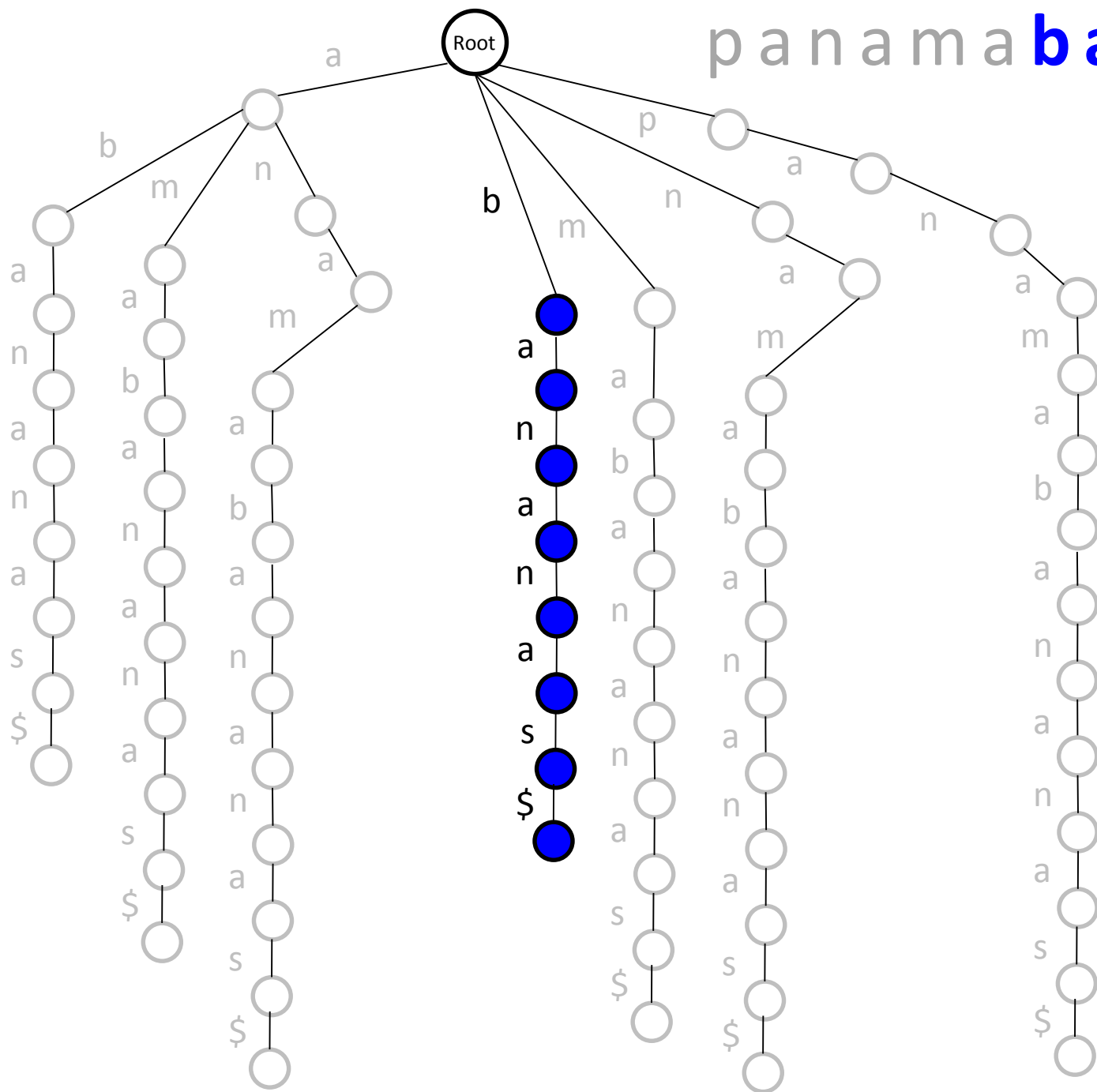
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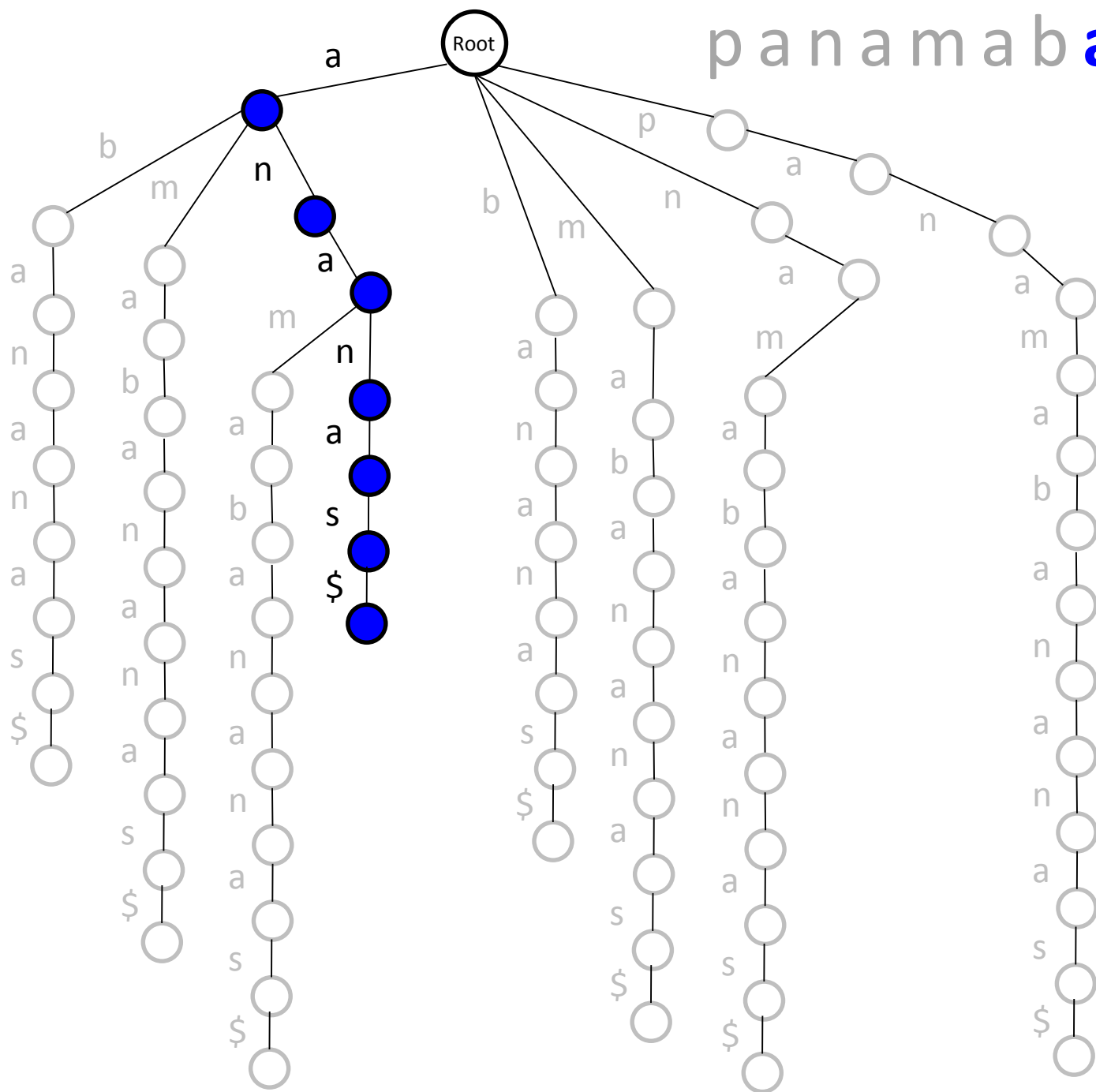
panama bananas \$



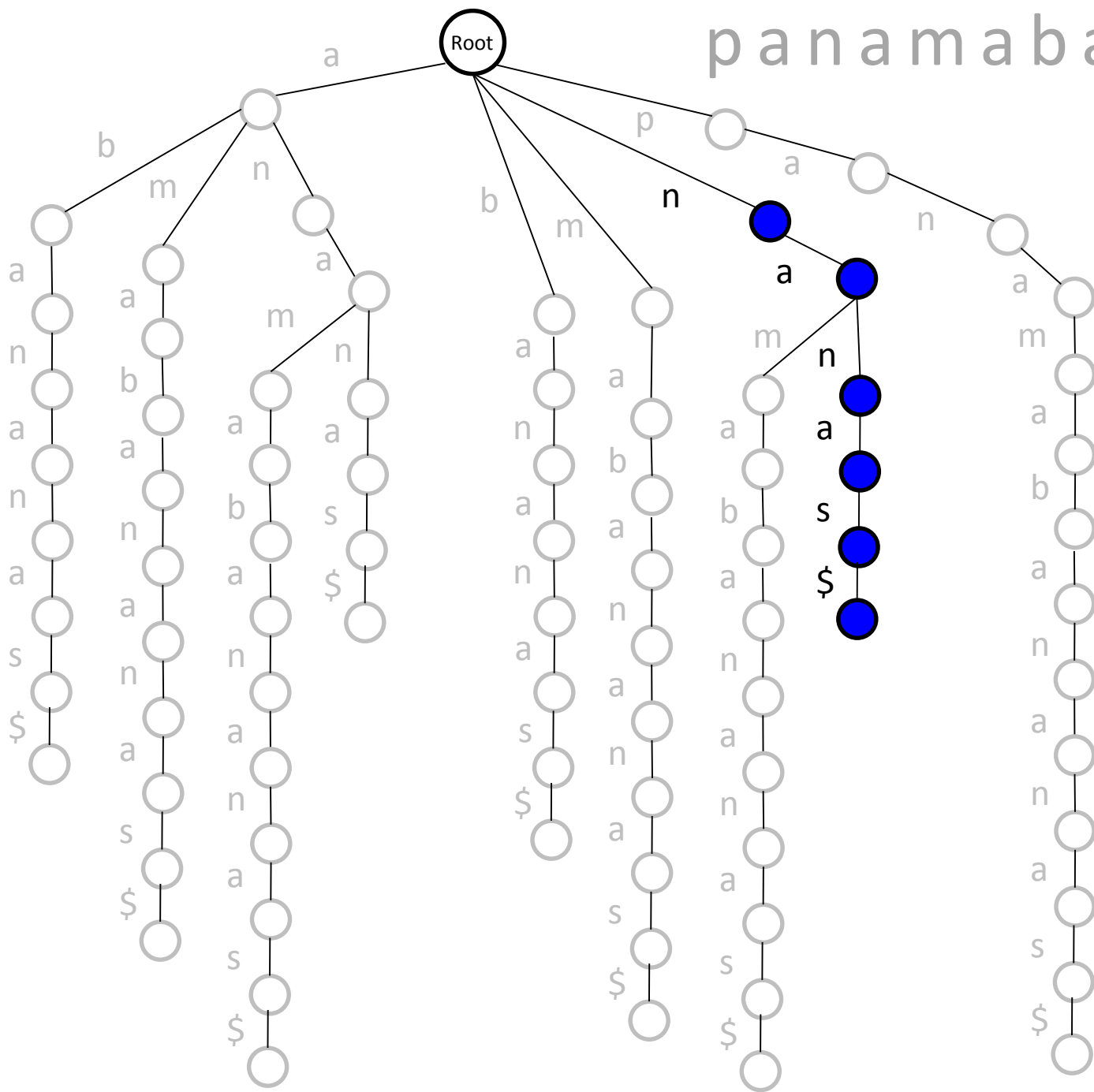
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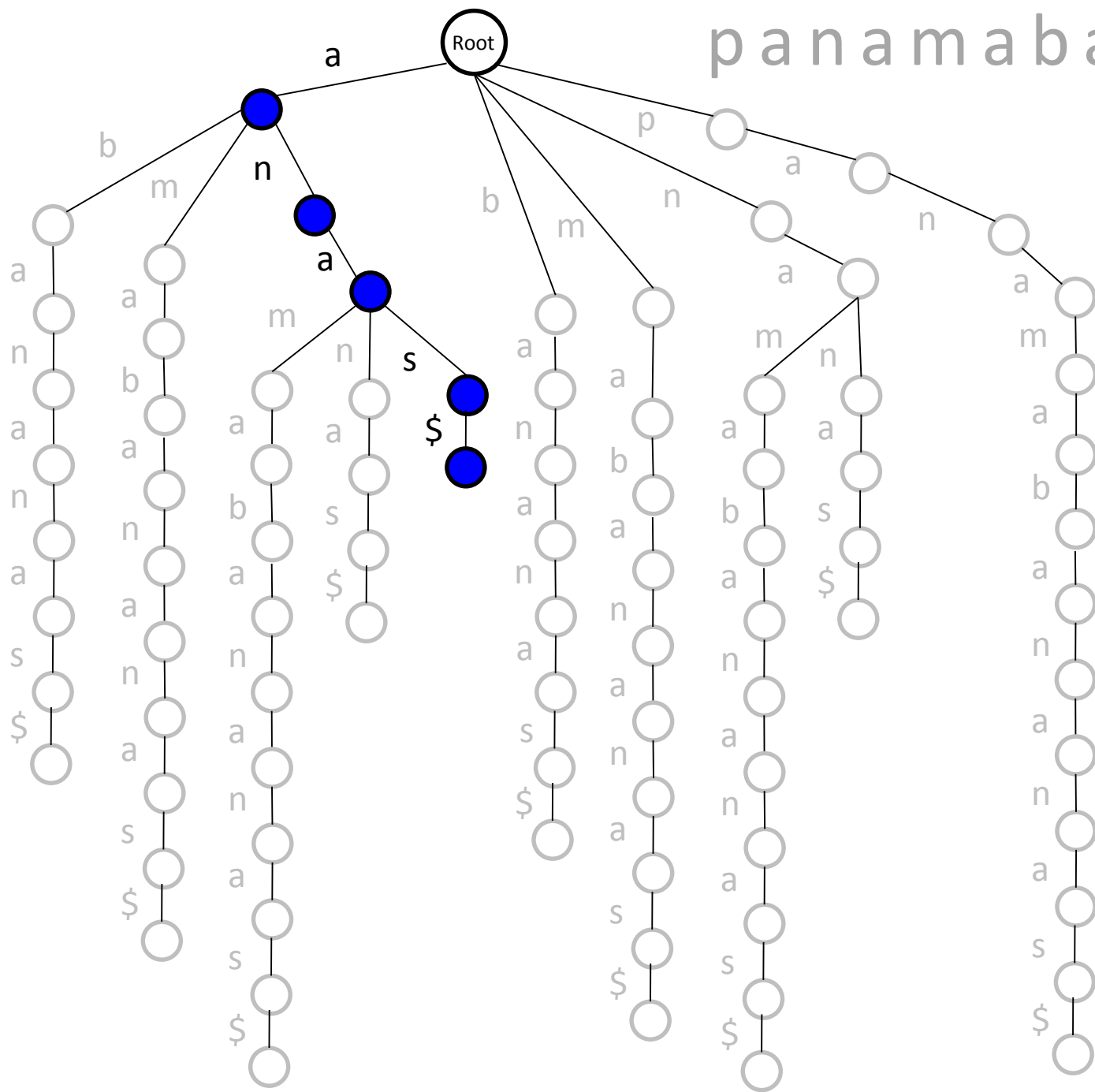
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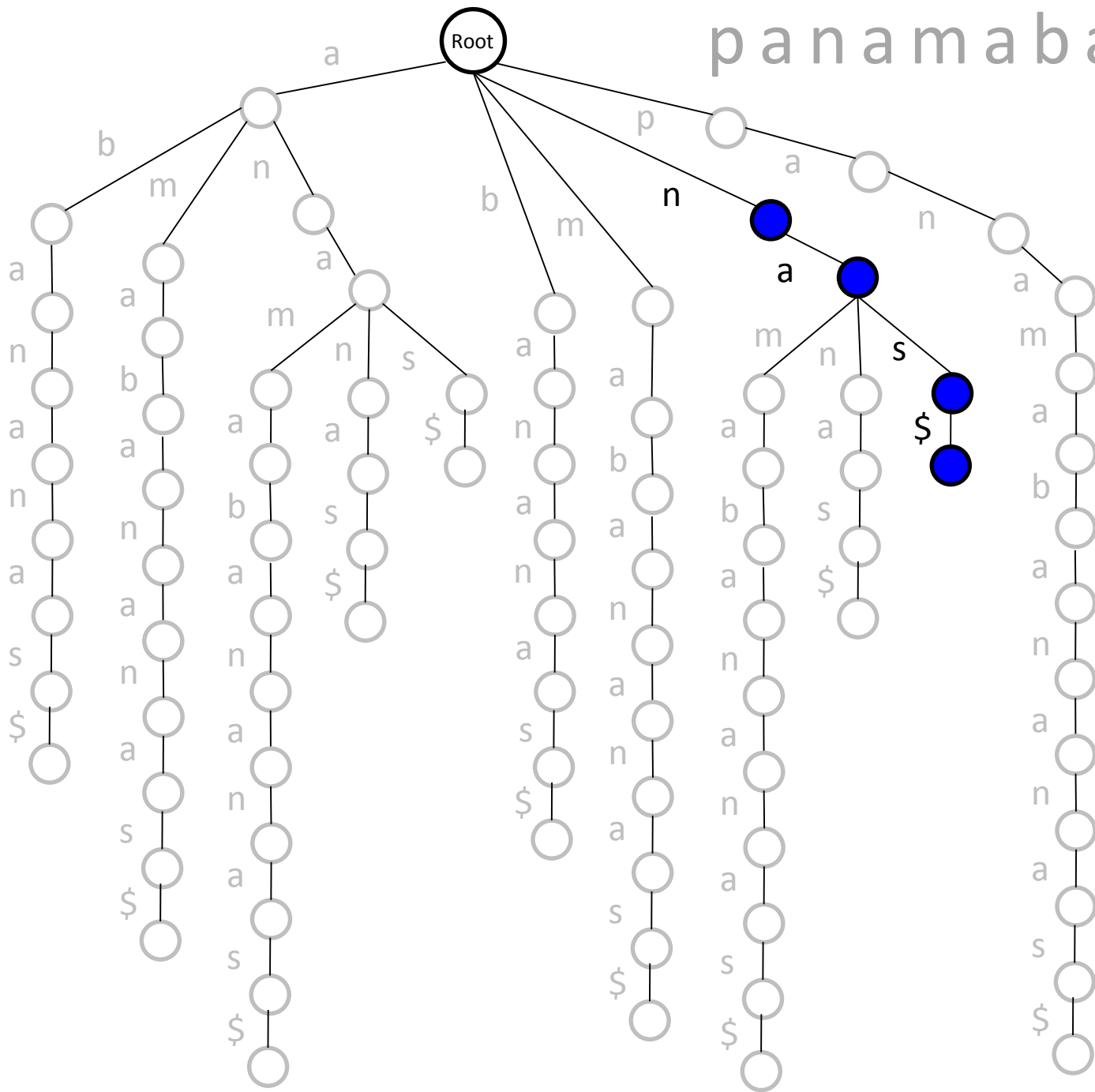
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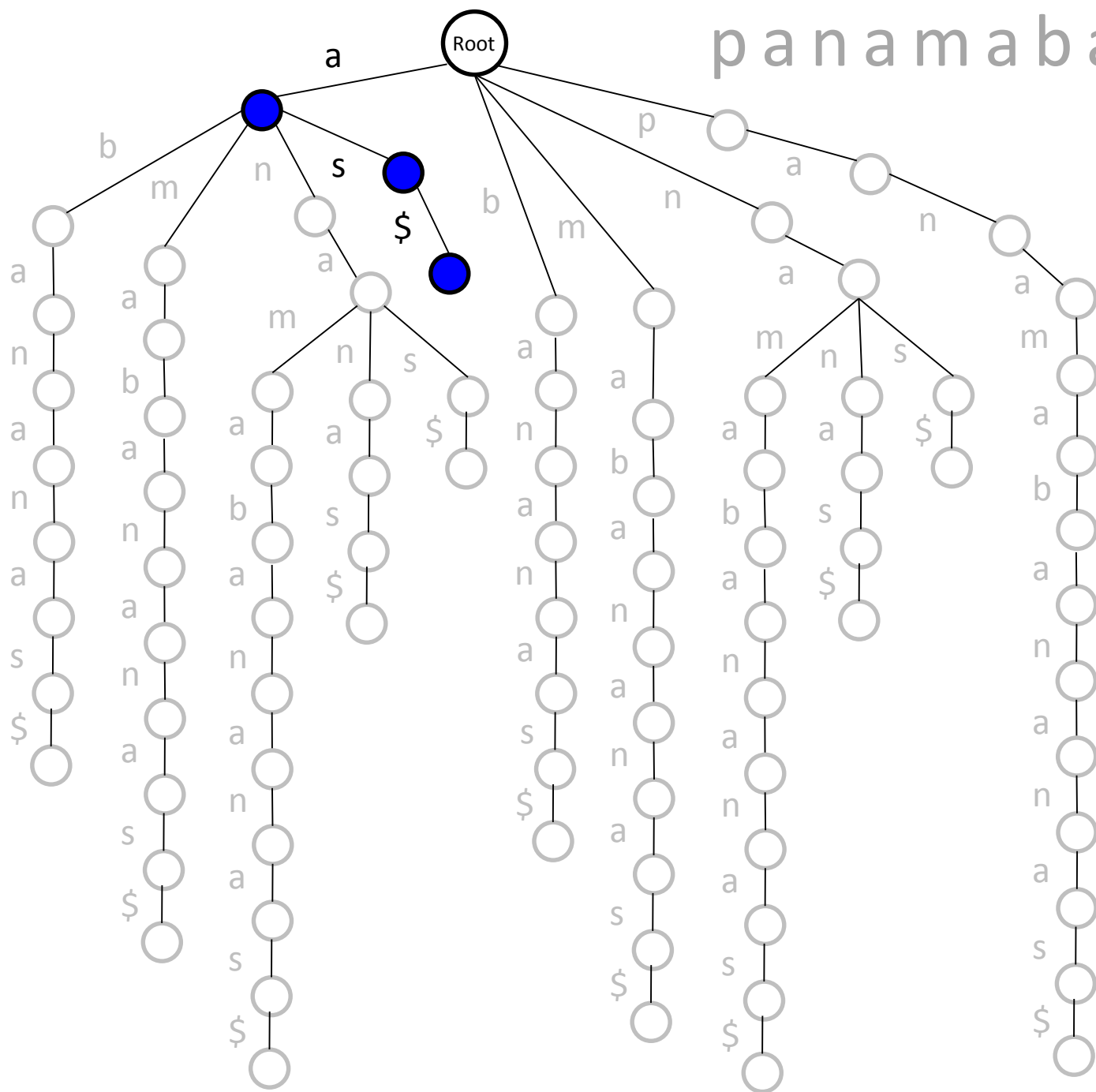
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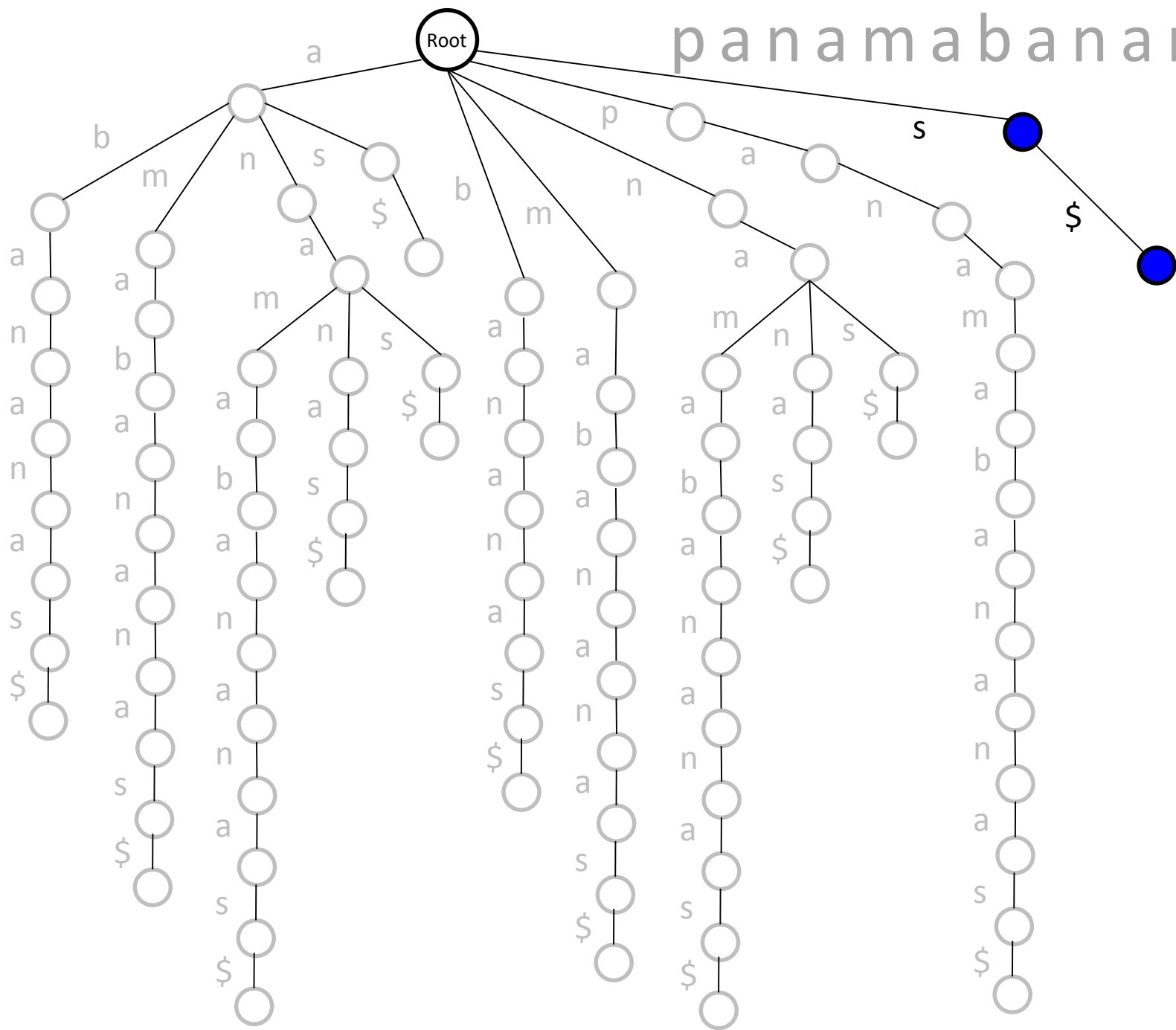
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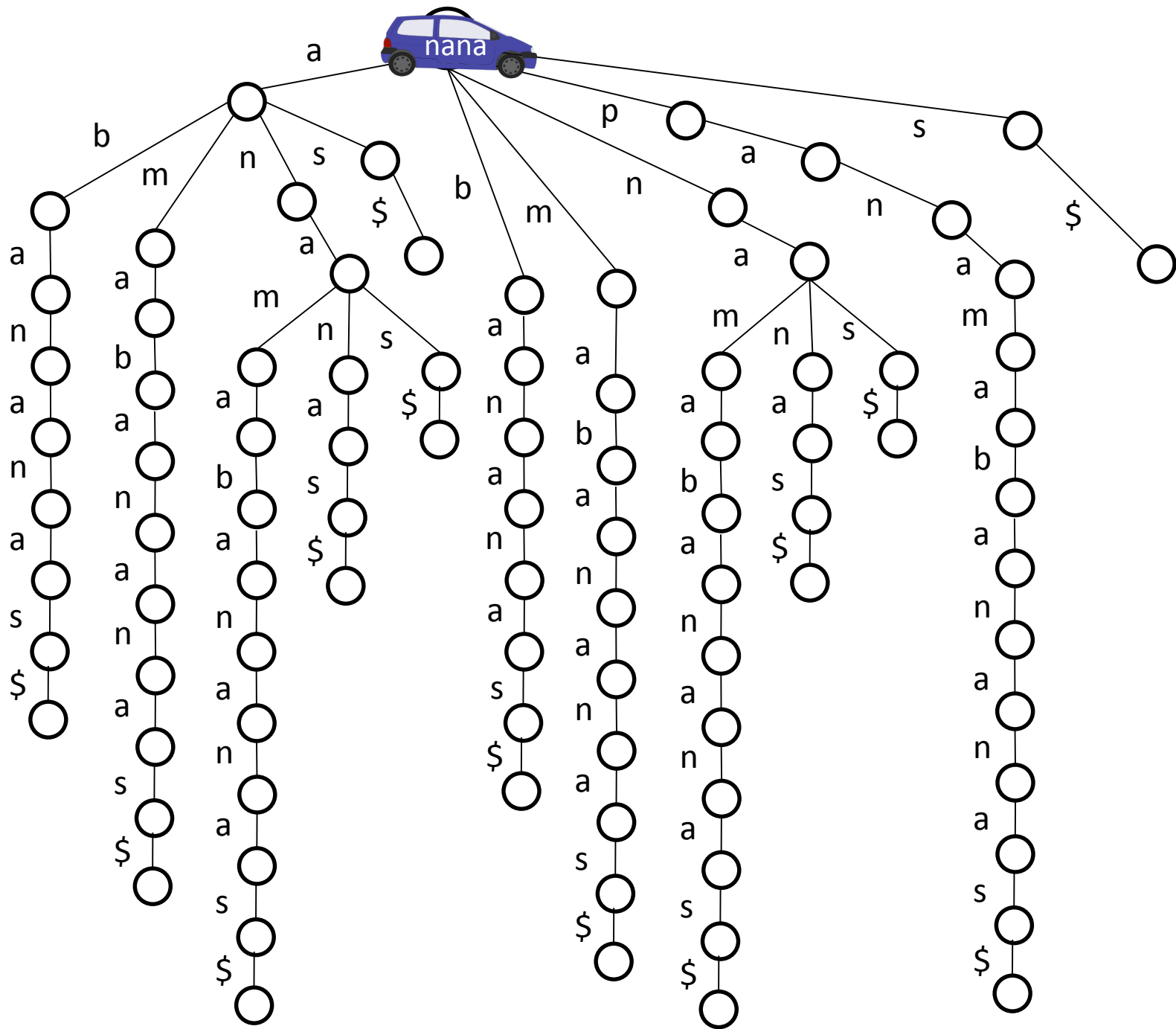


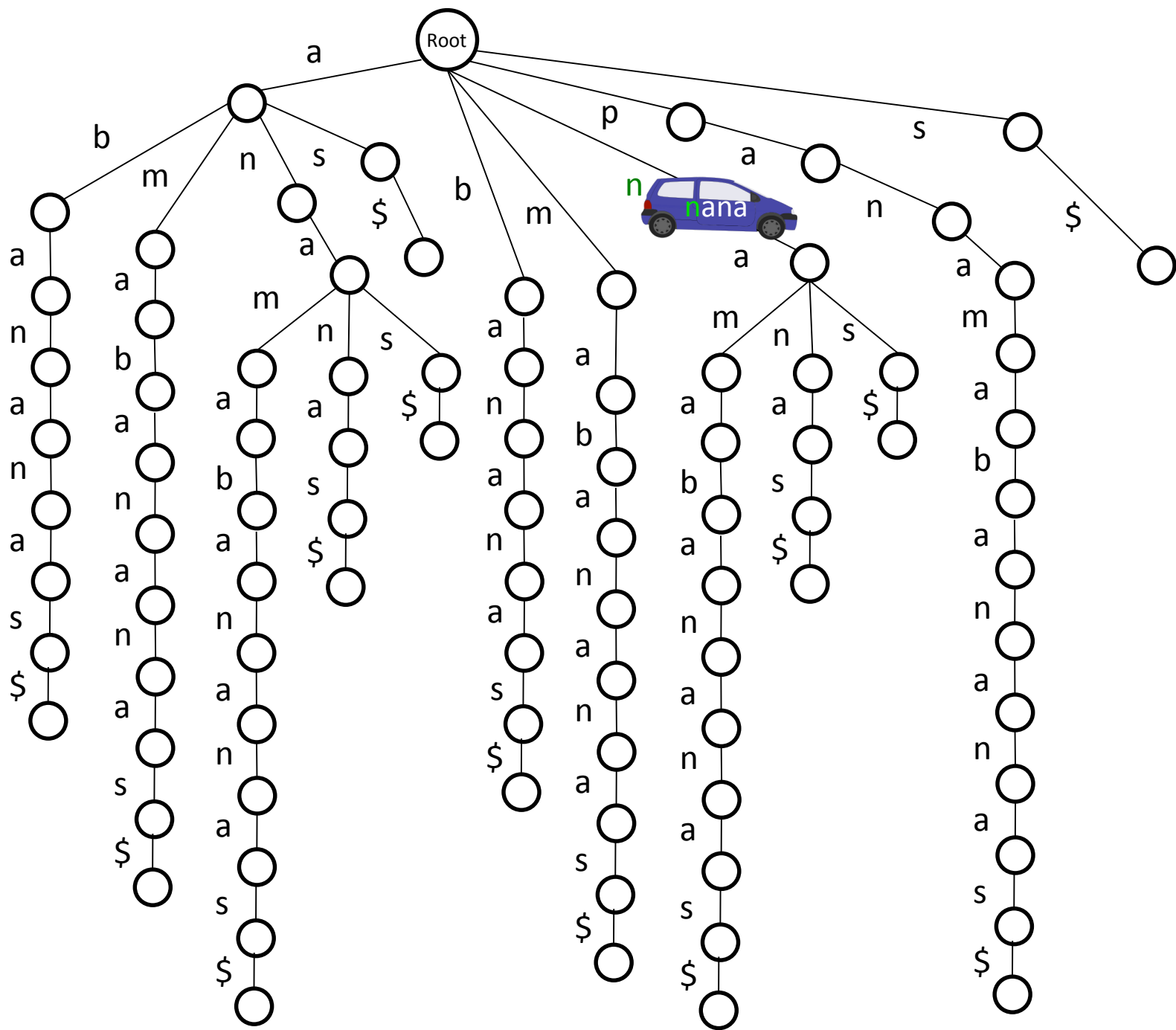
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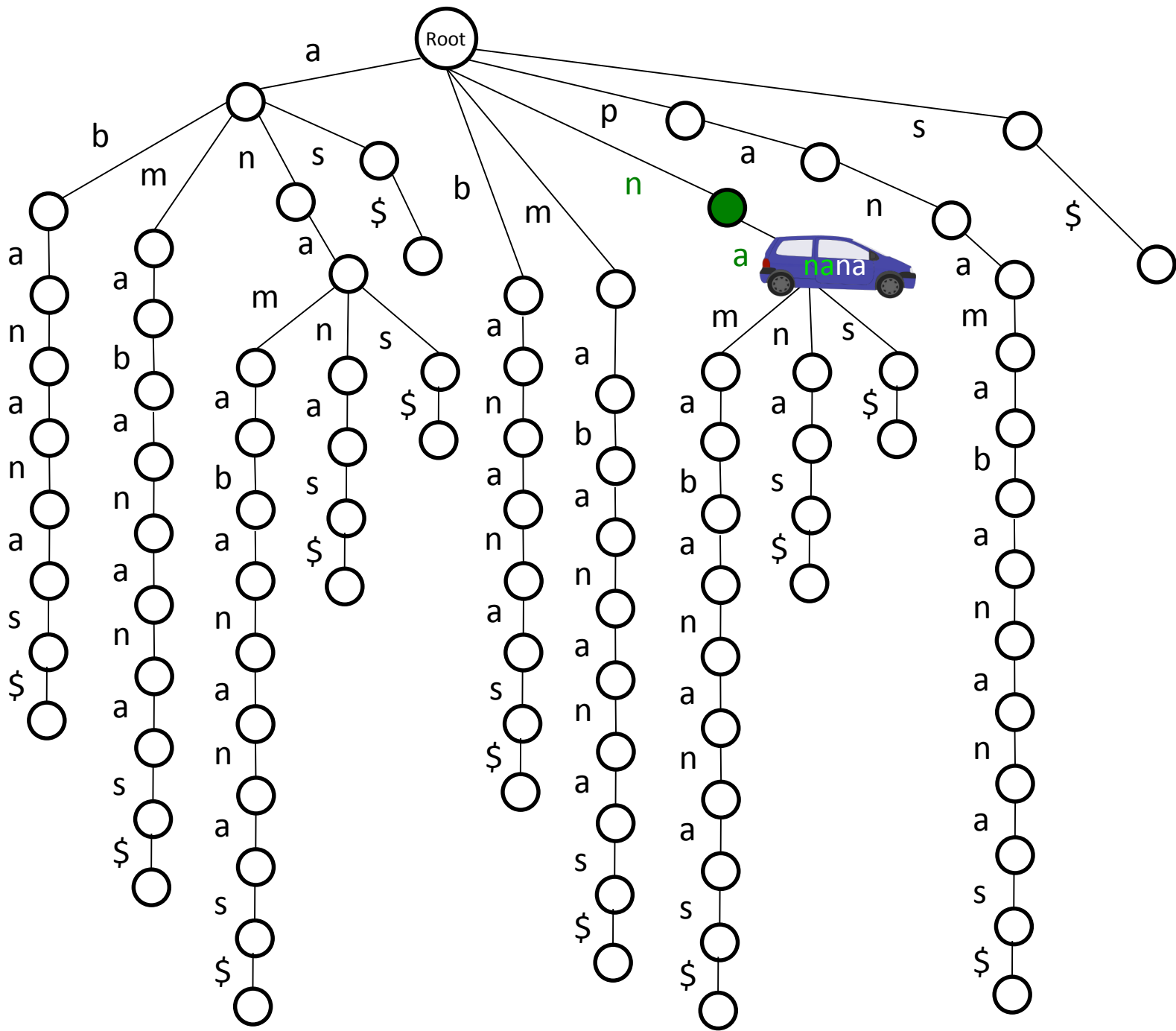


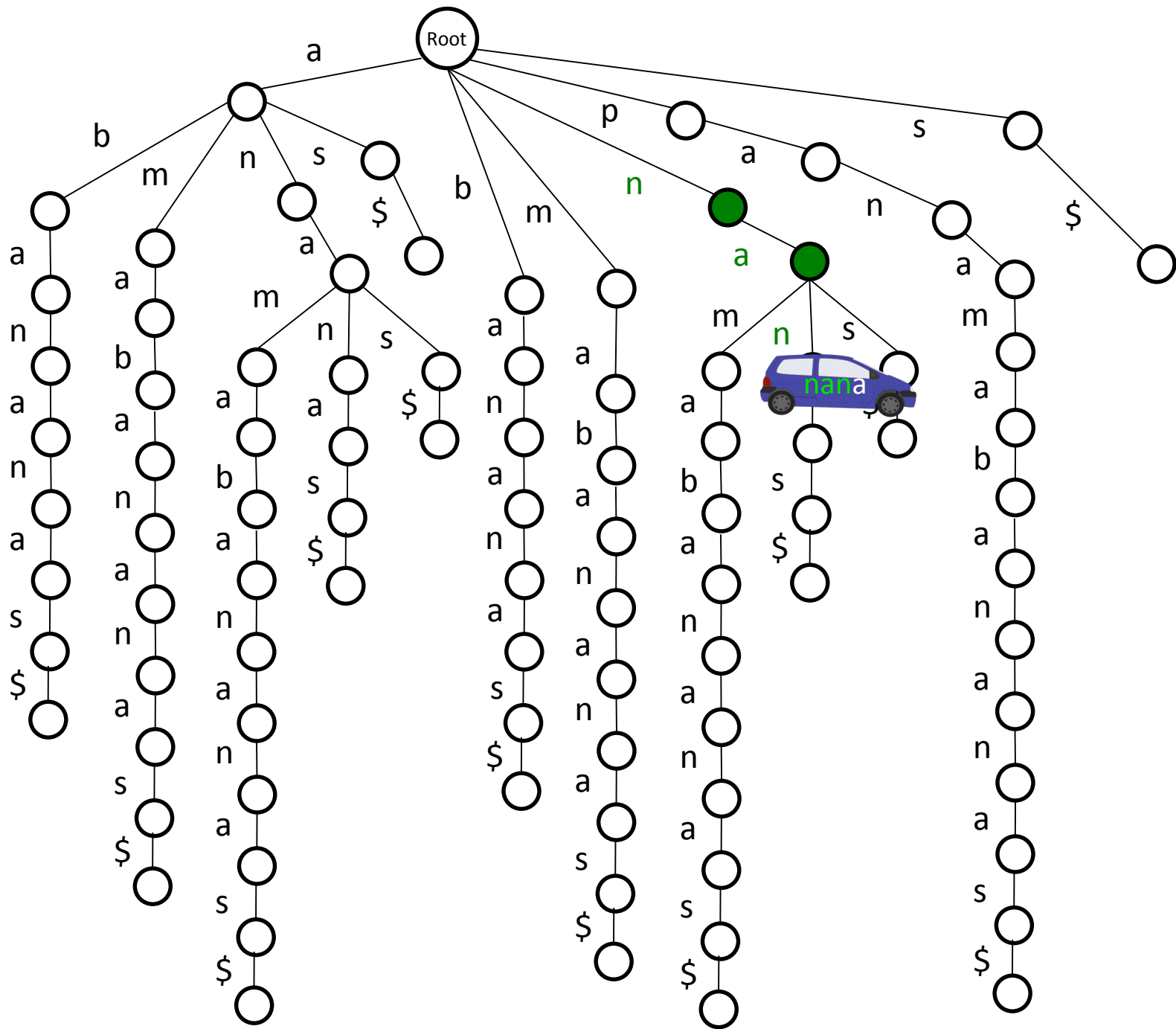
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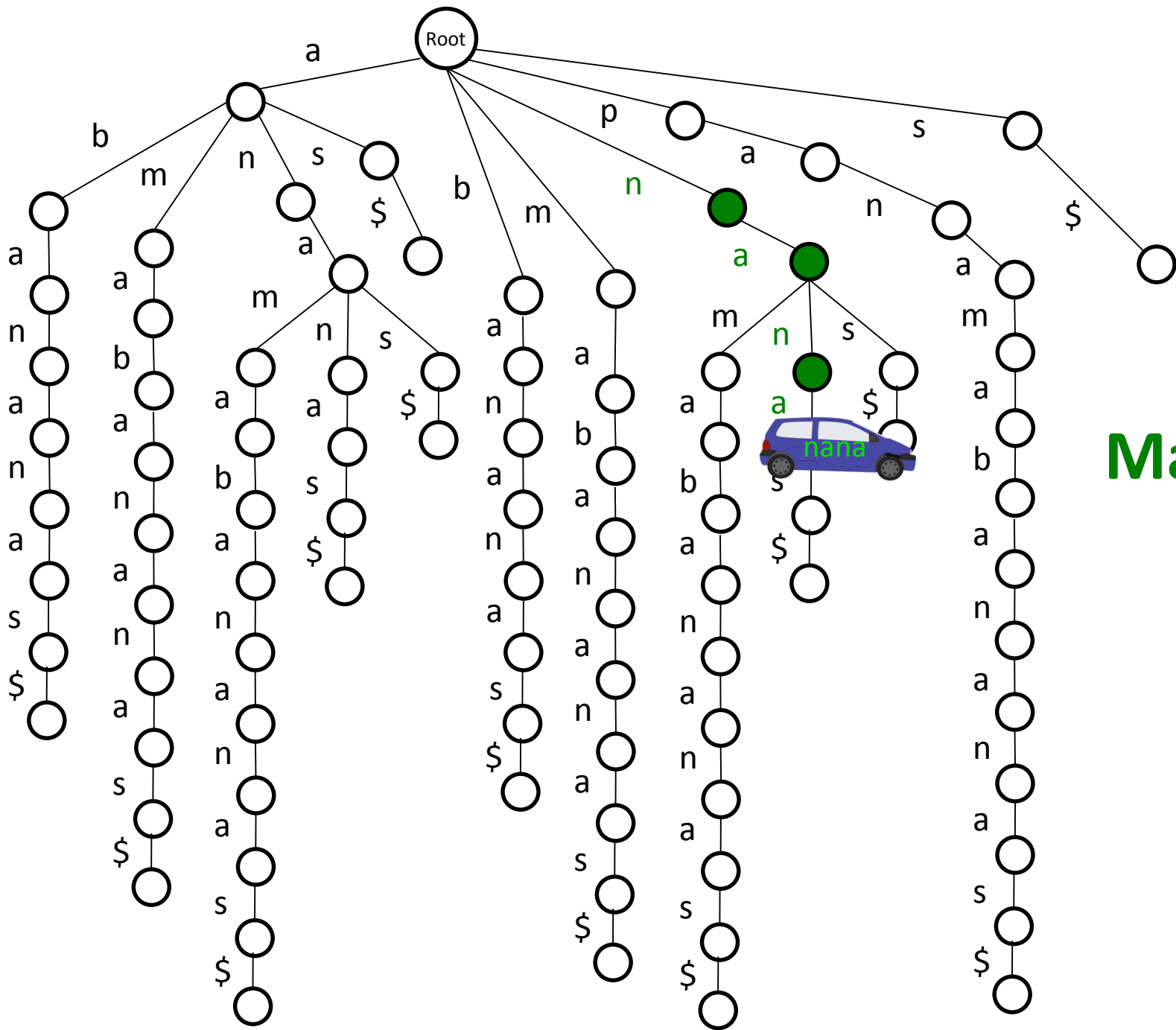


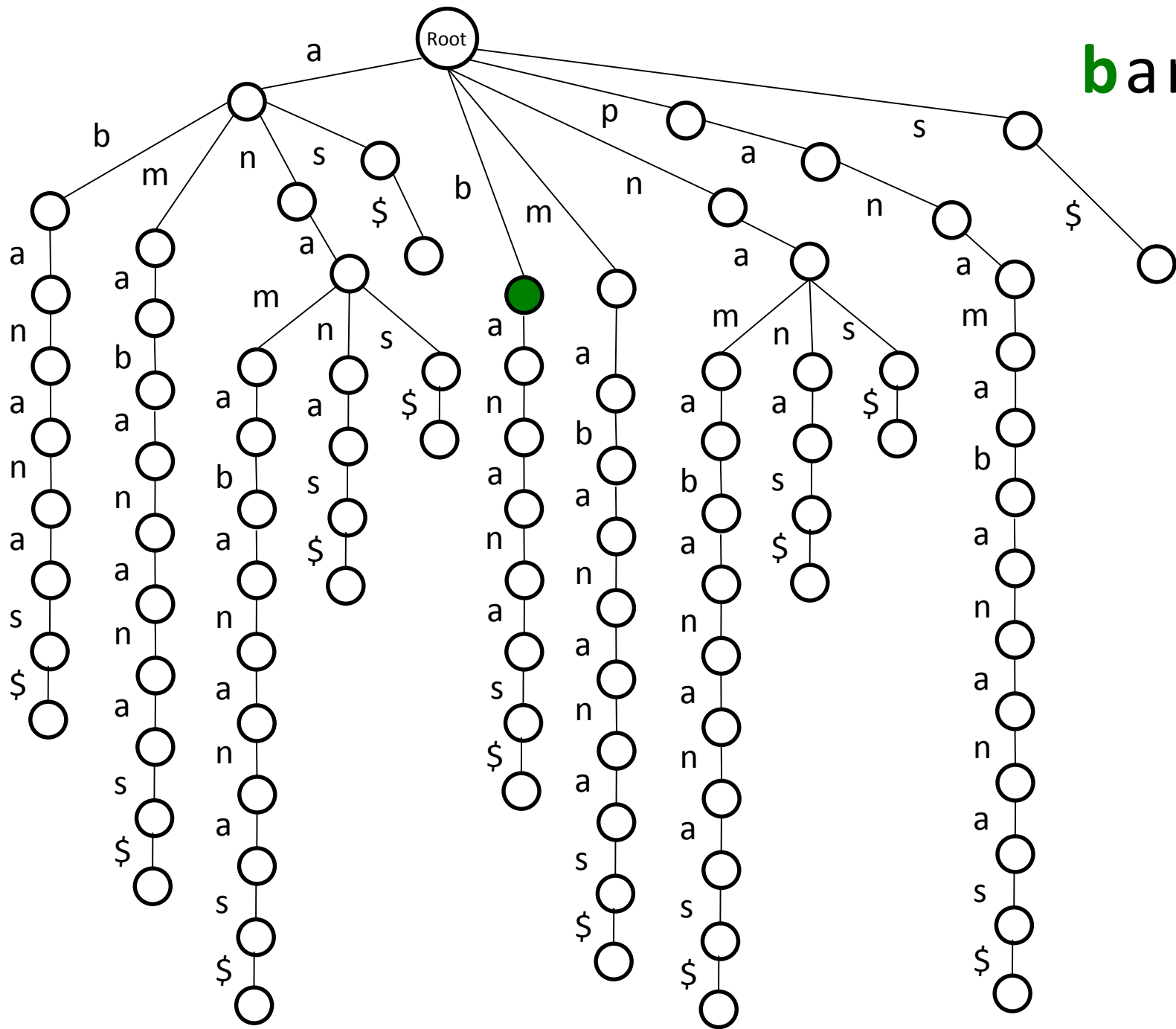




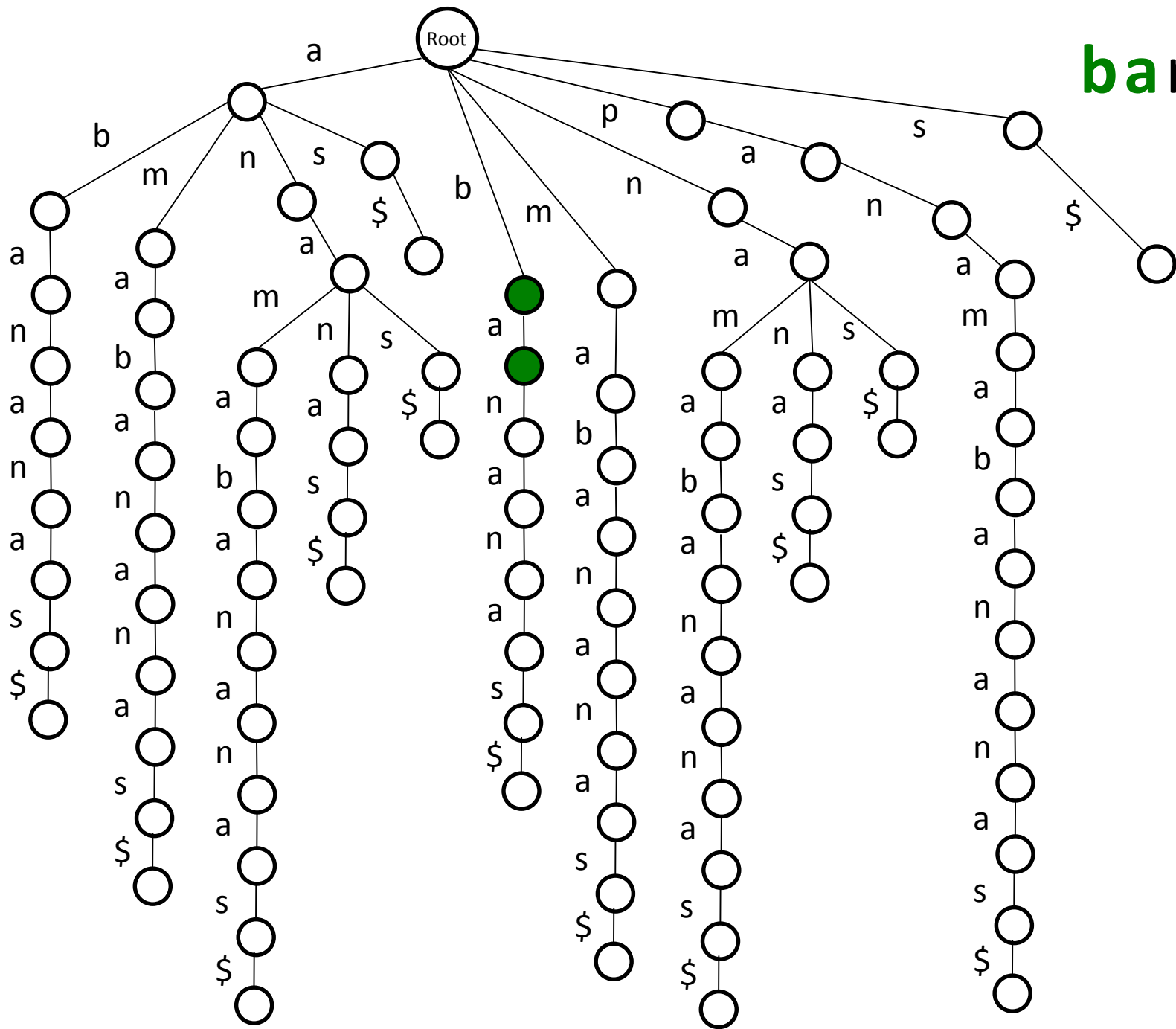








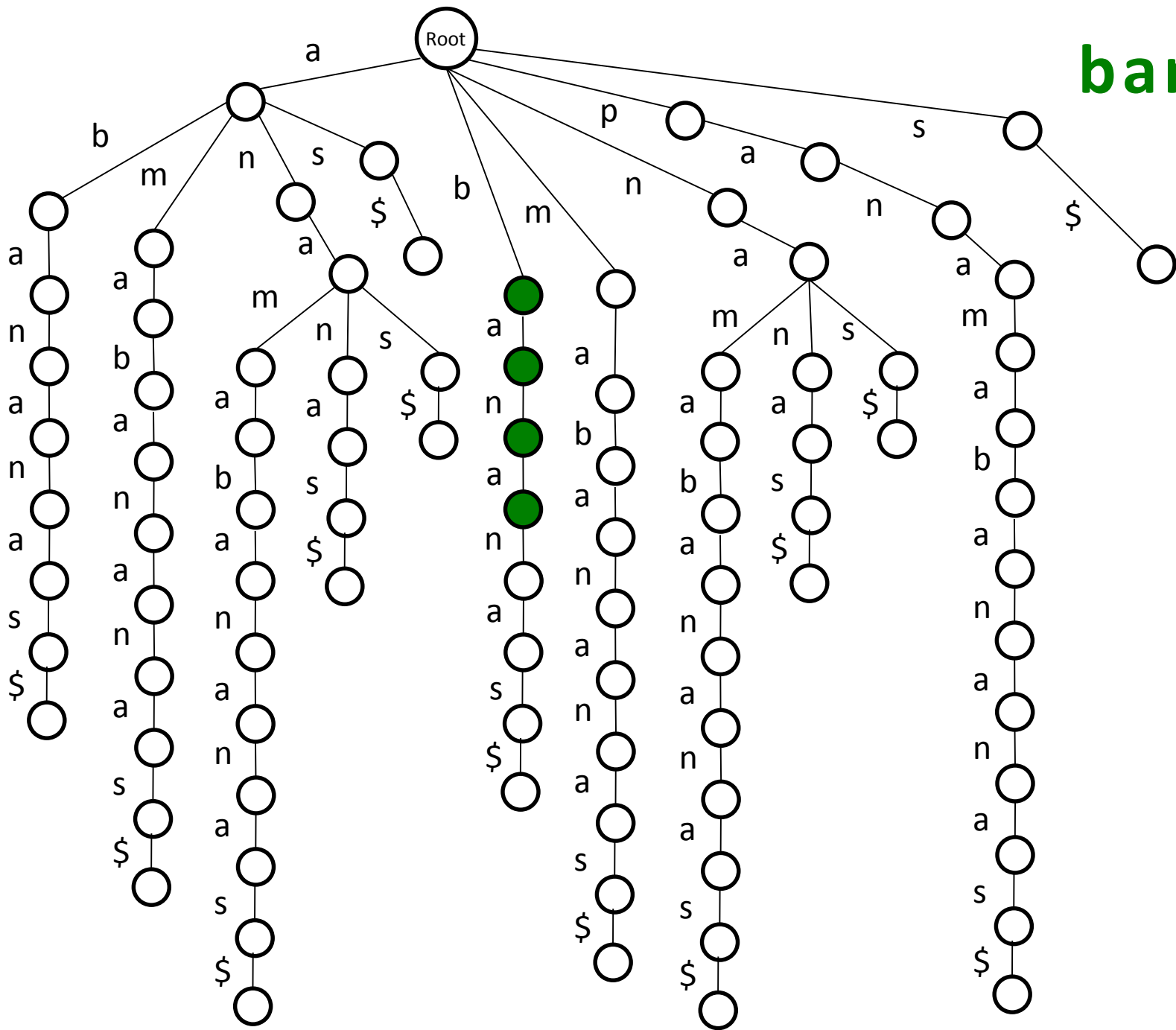
banana



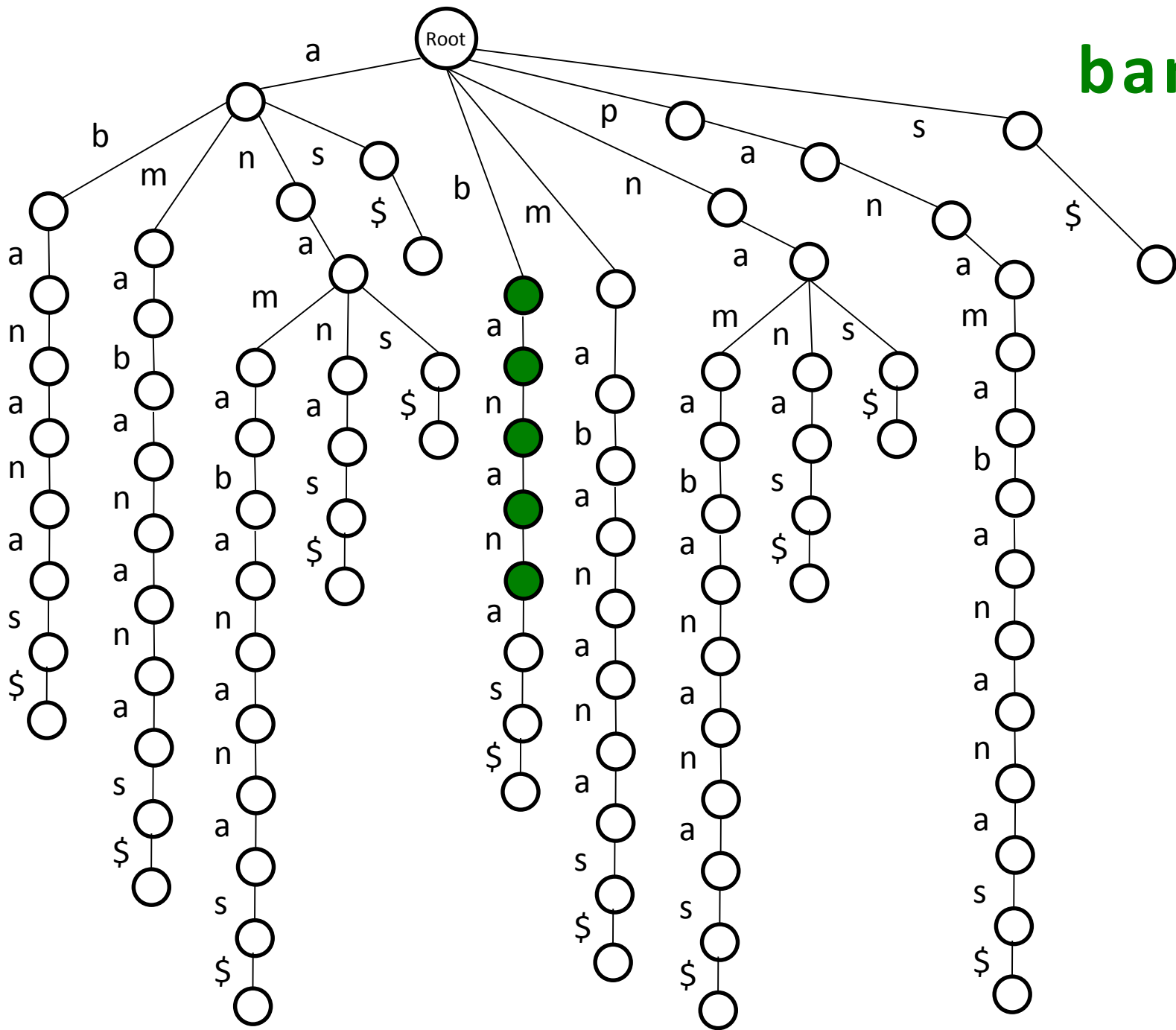
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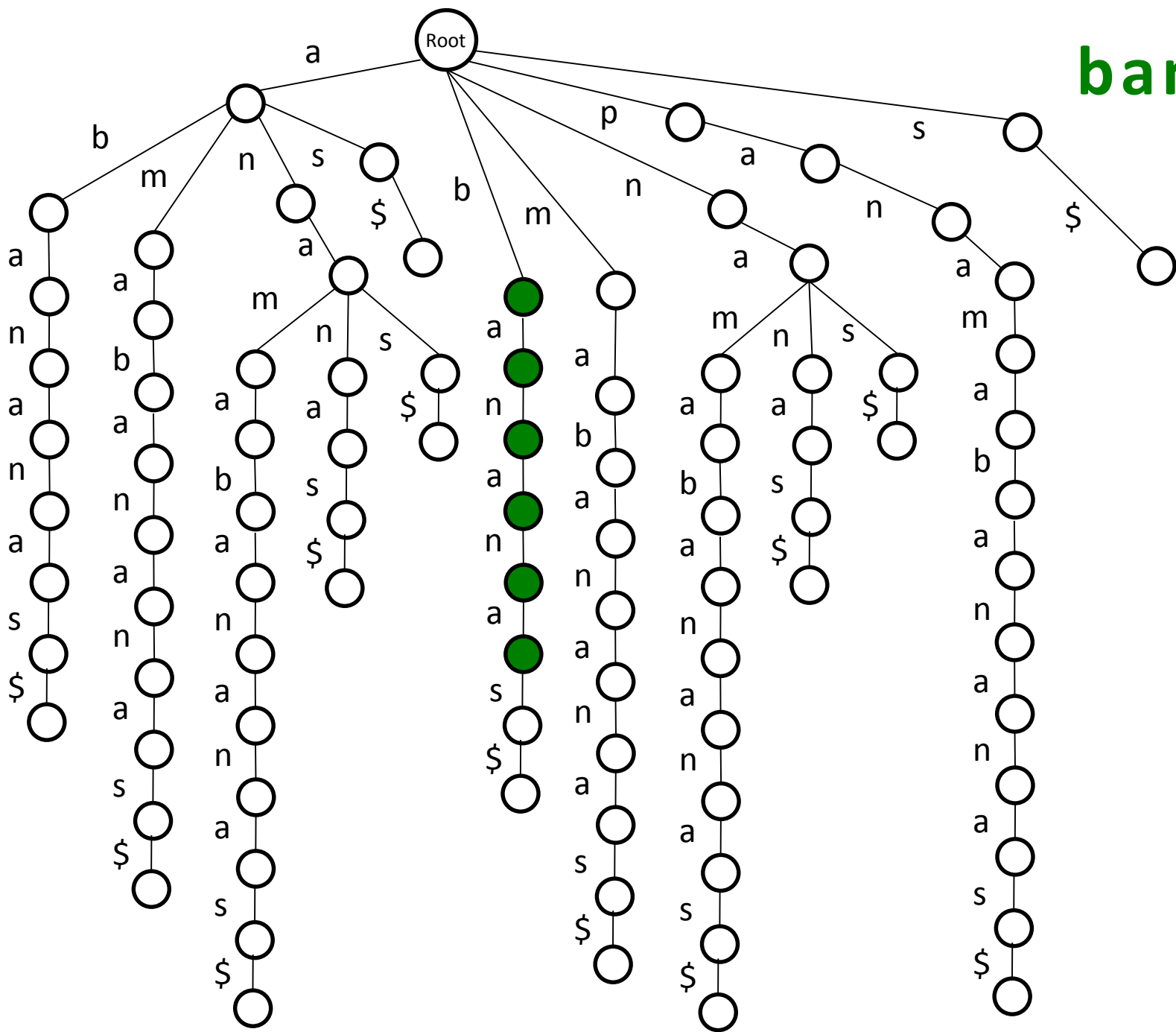
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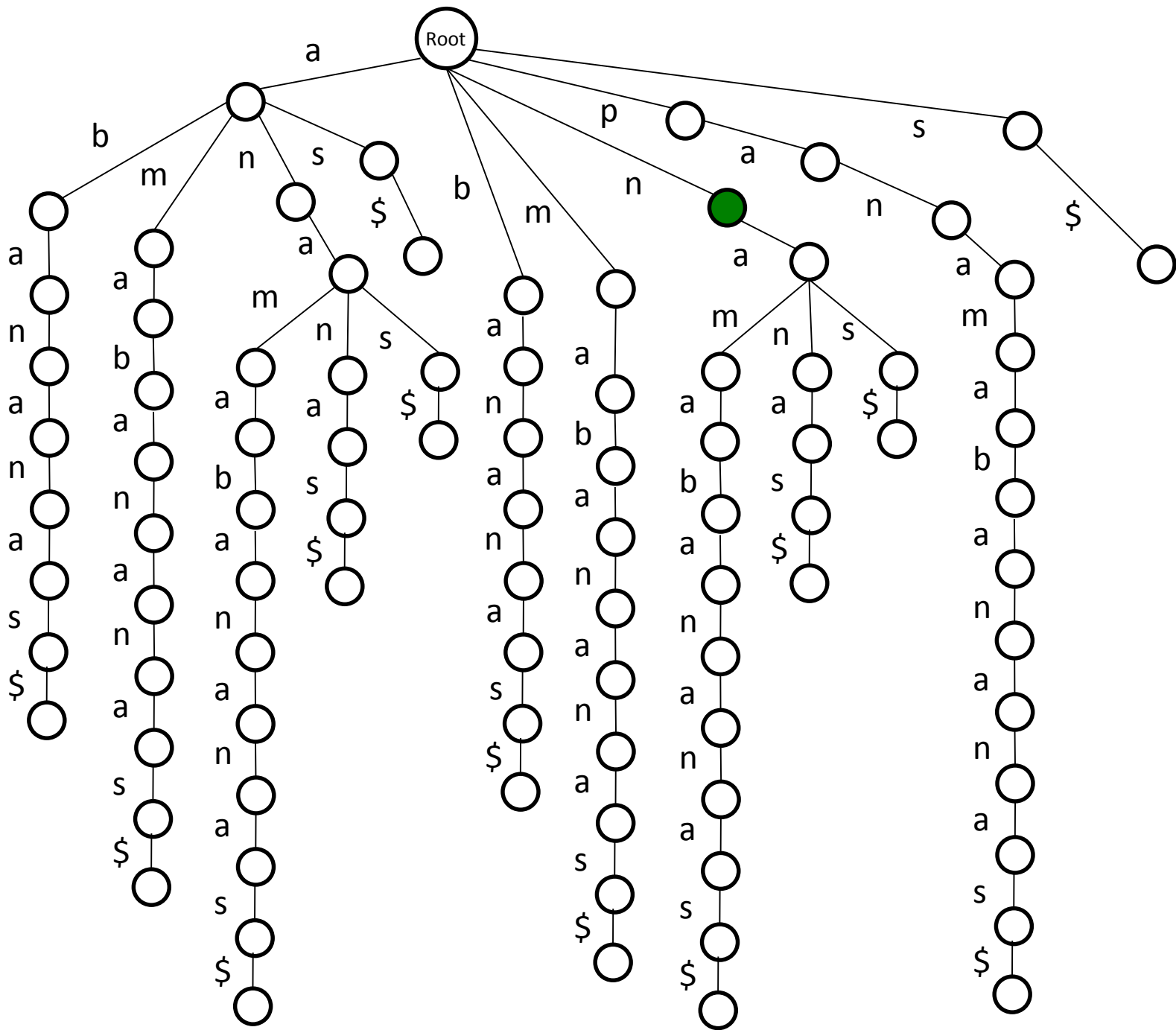
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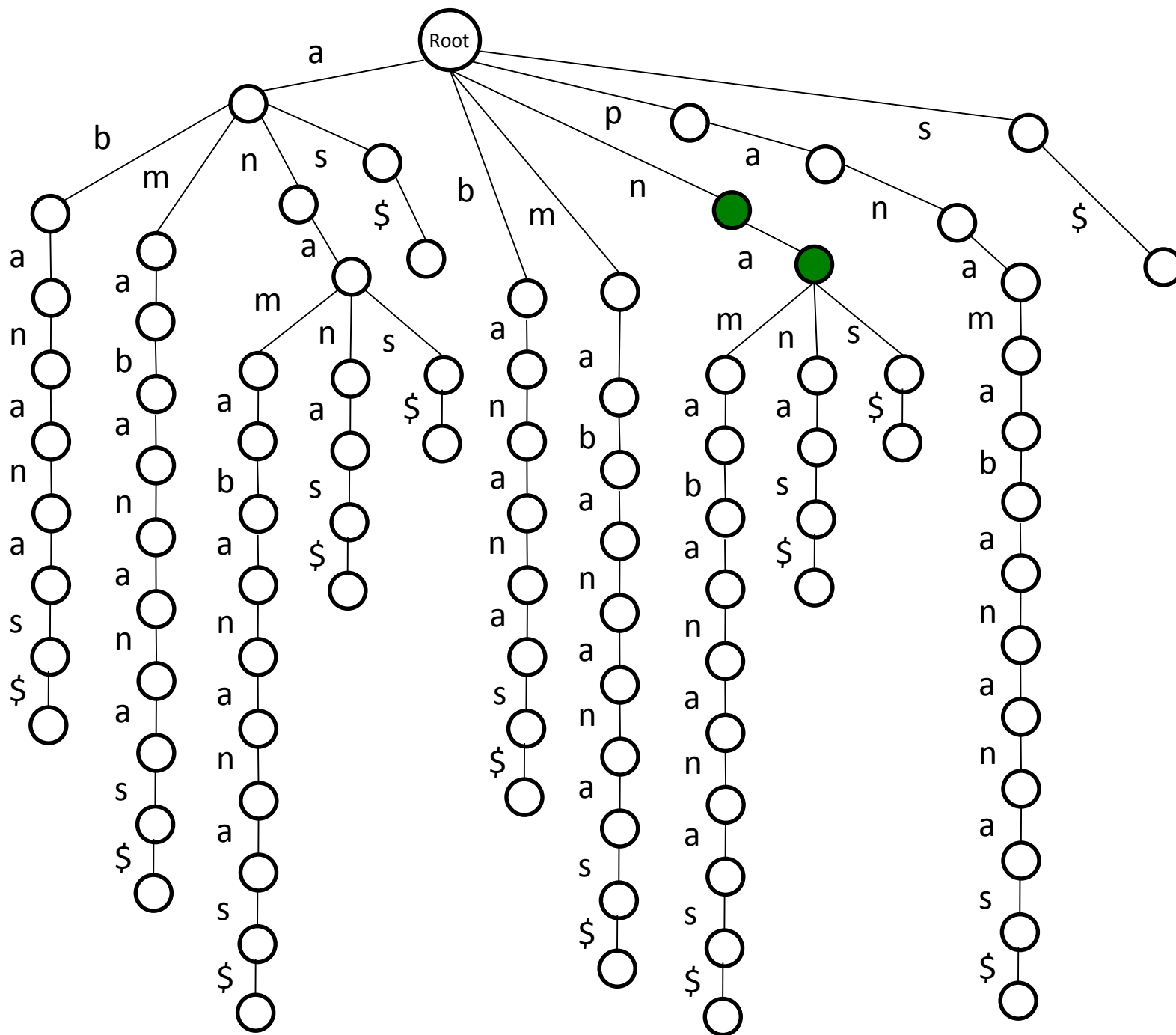
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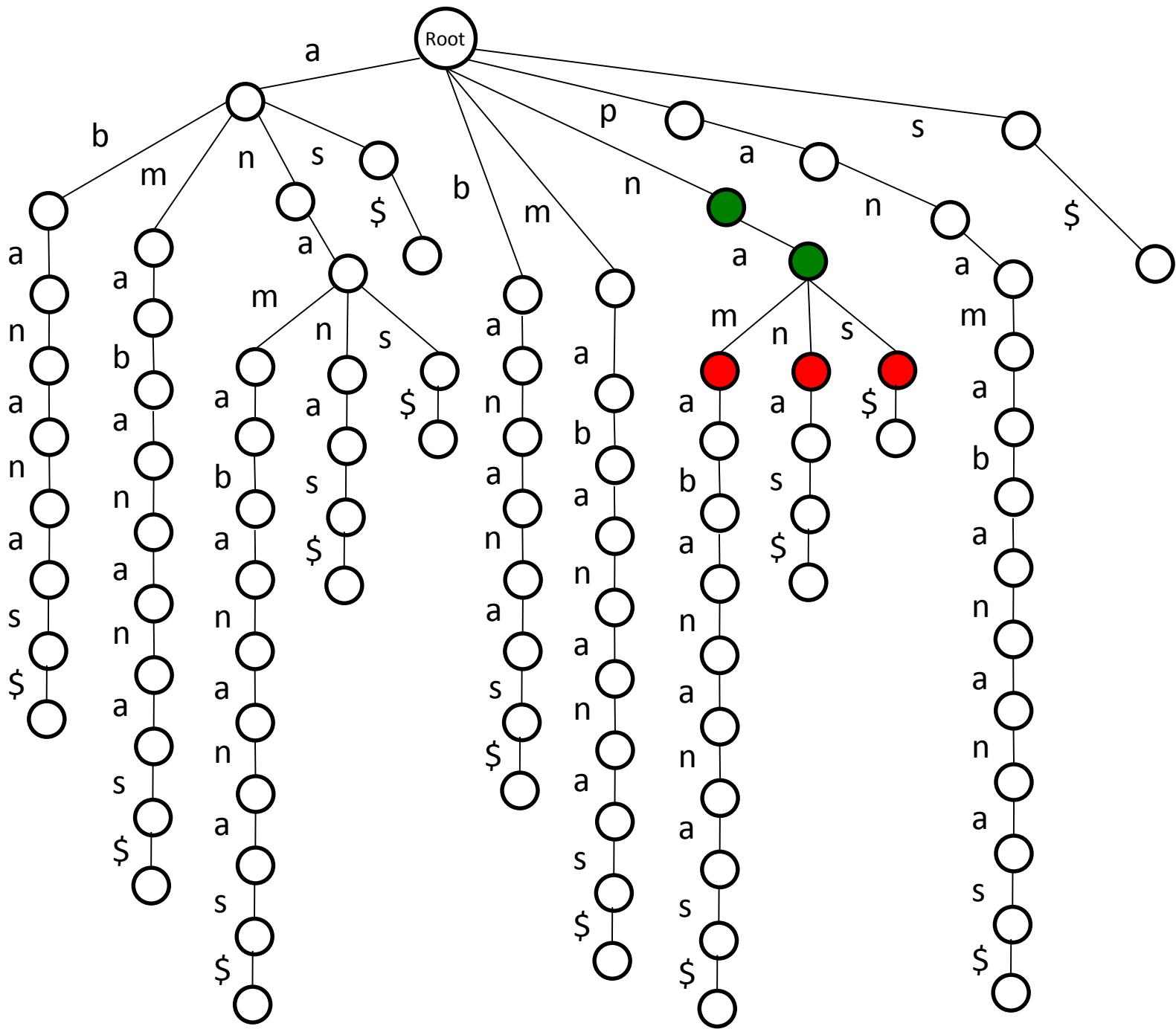
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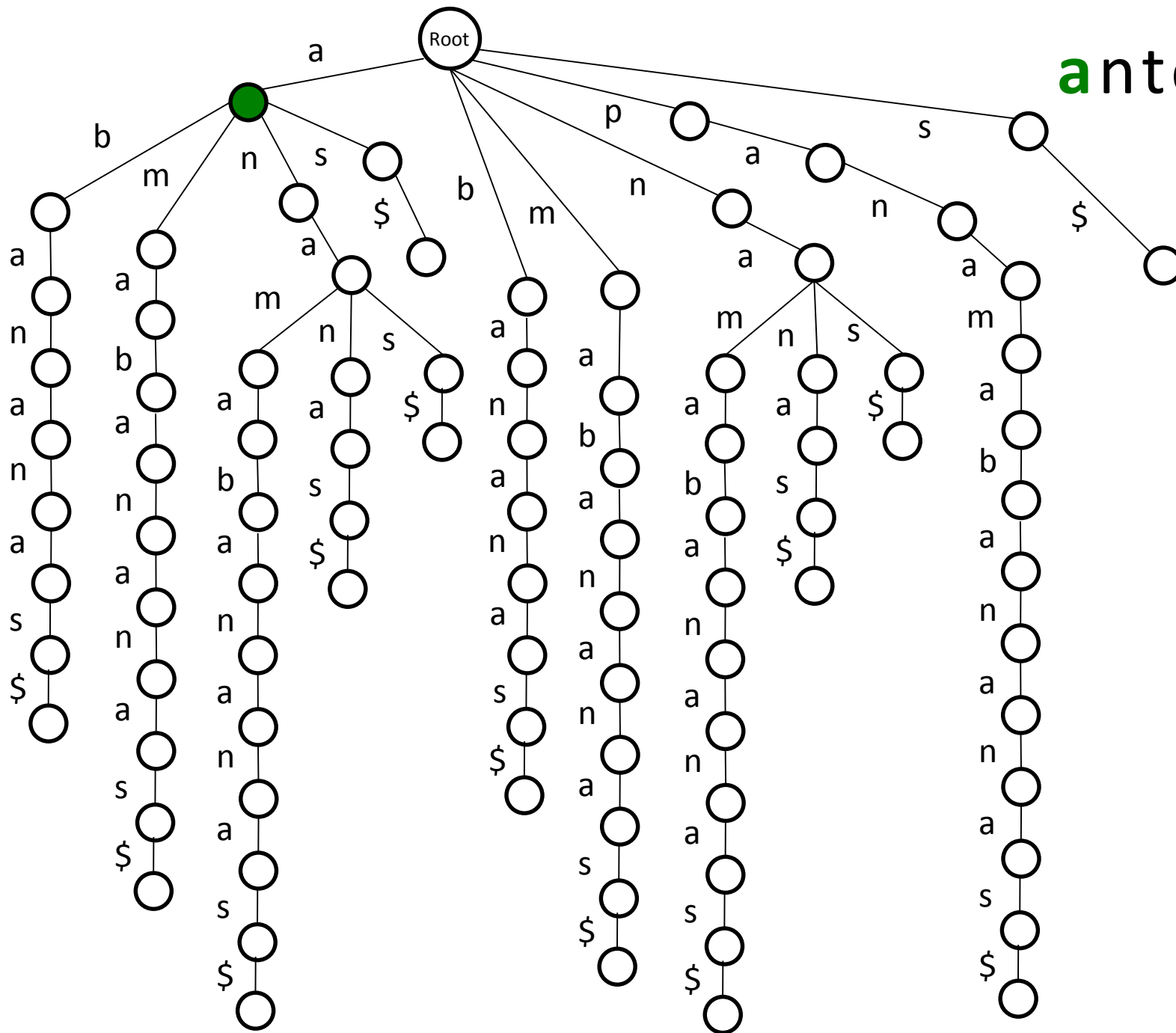
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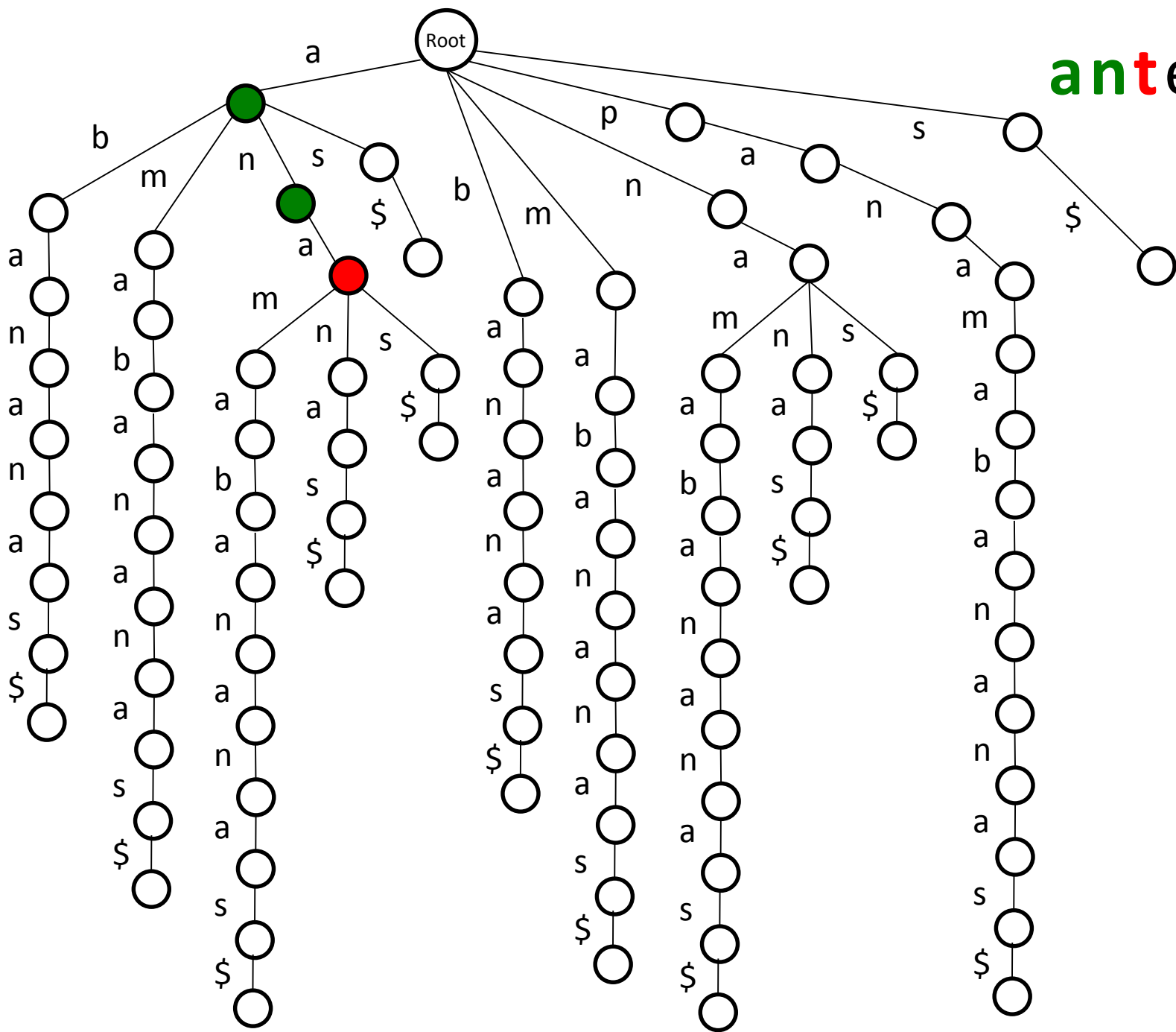
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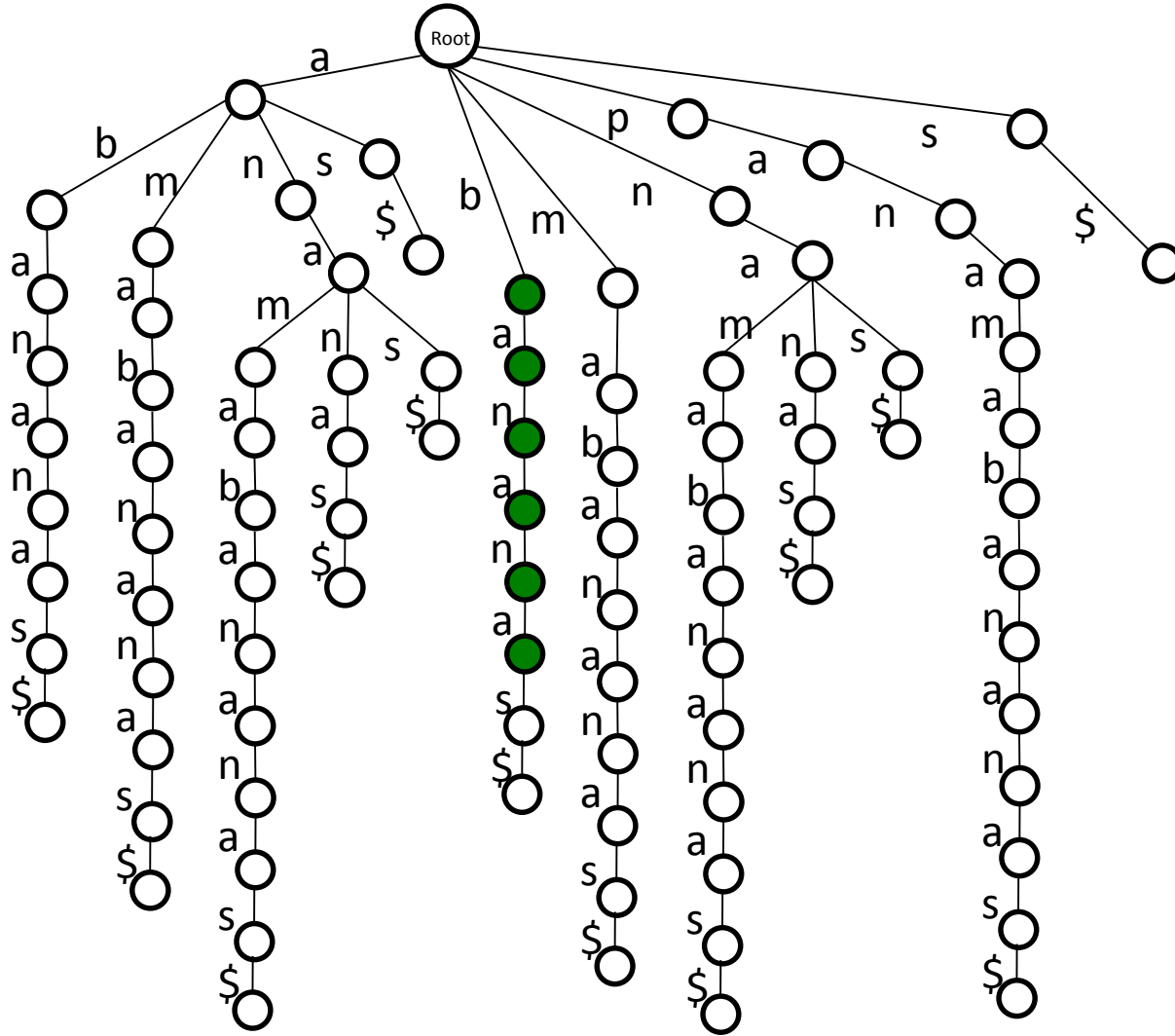


antenna

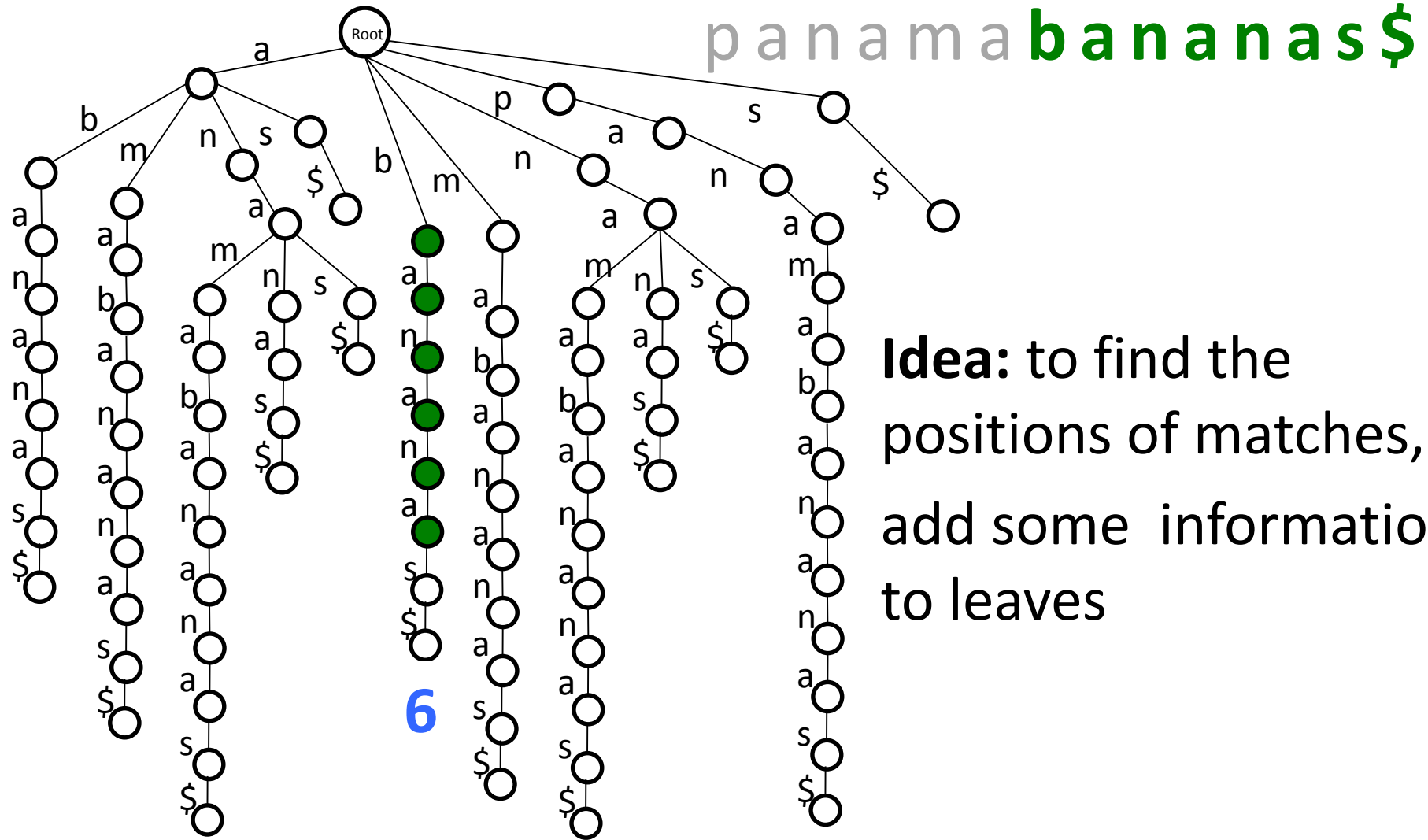


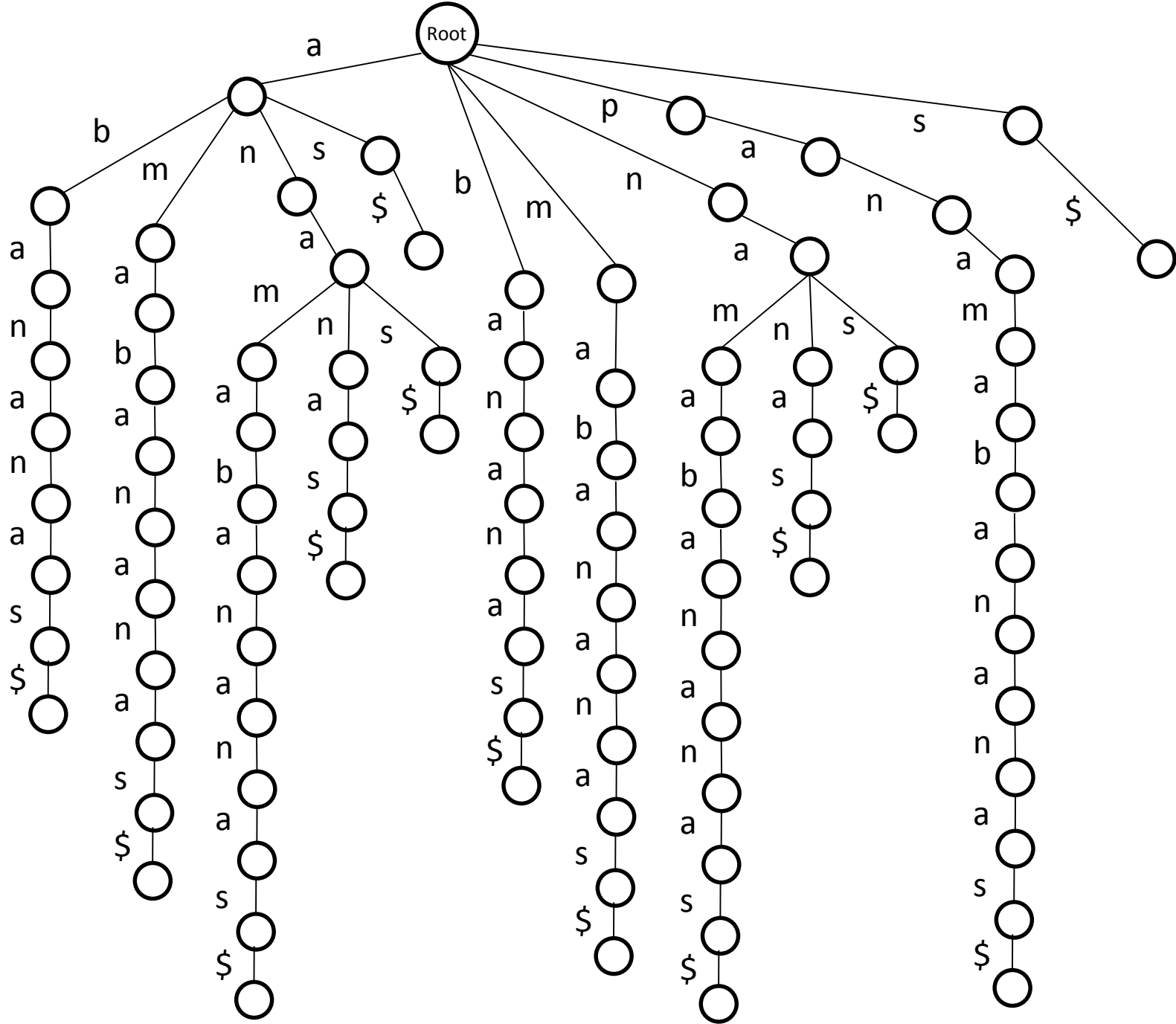
Where Are the Matches???

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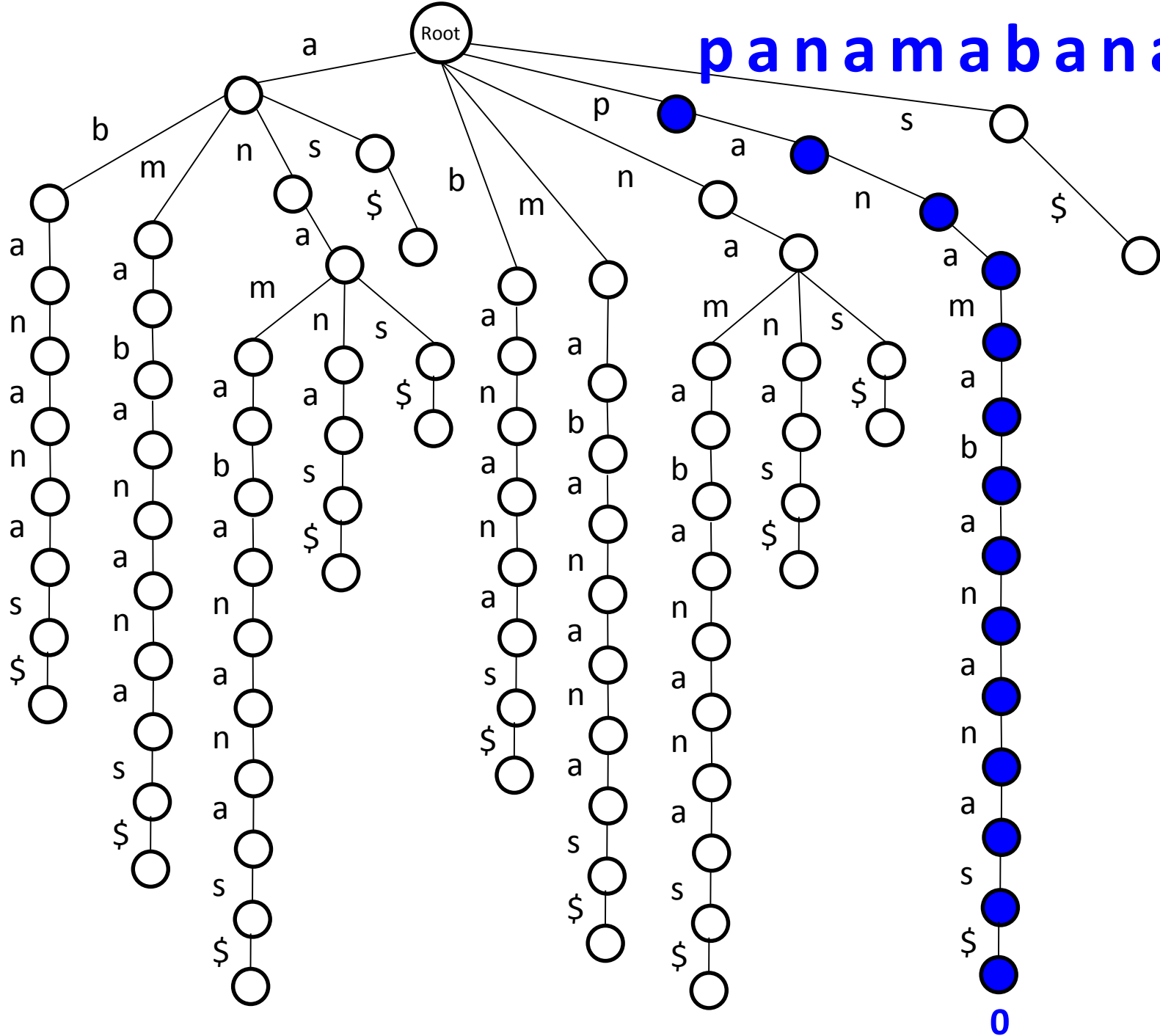


Where Are the Matches???

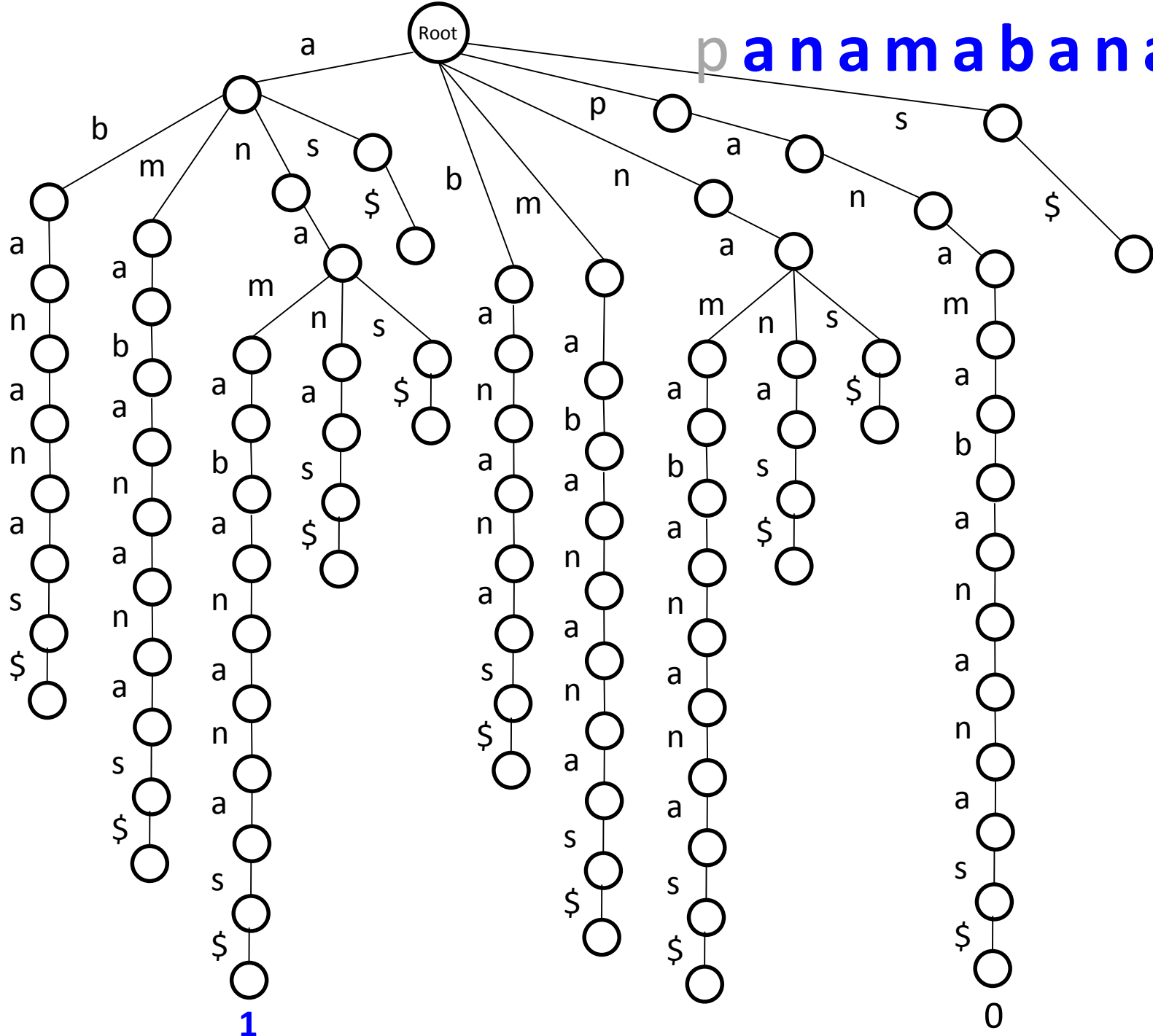


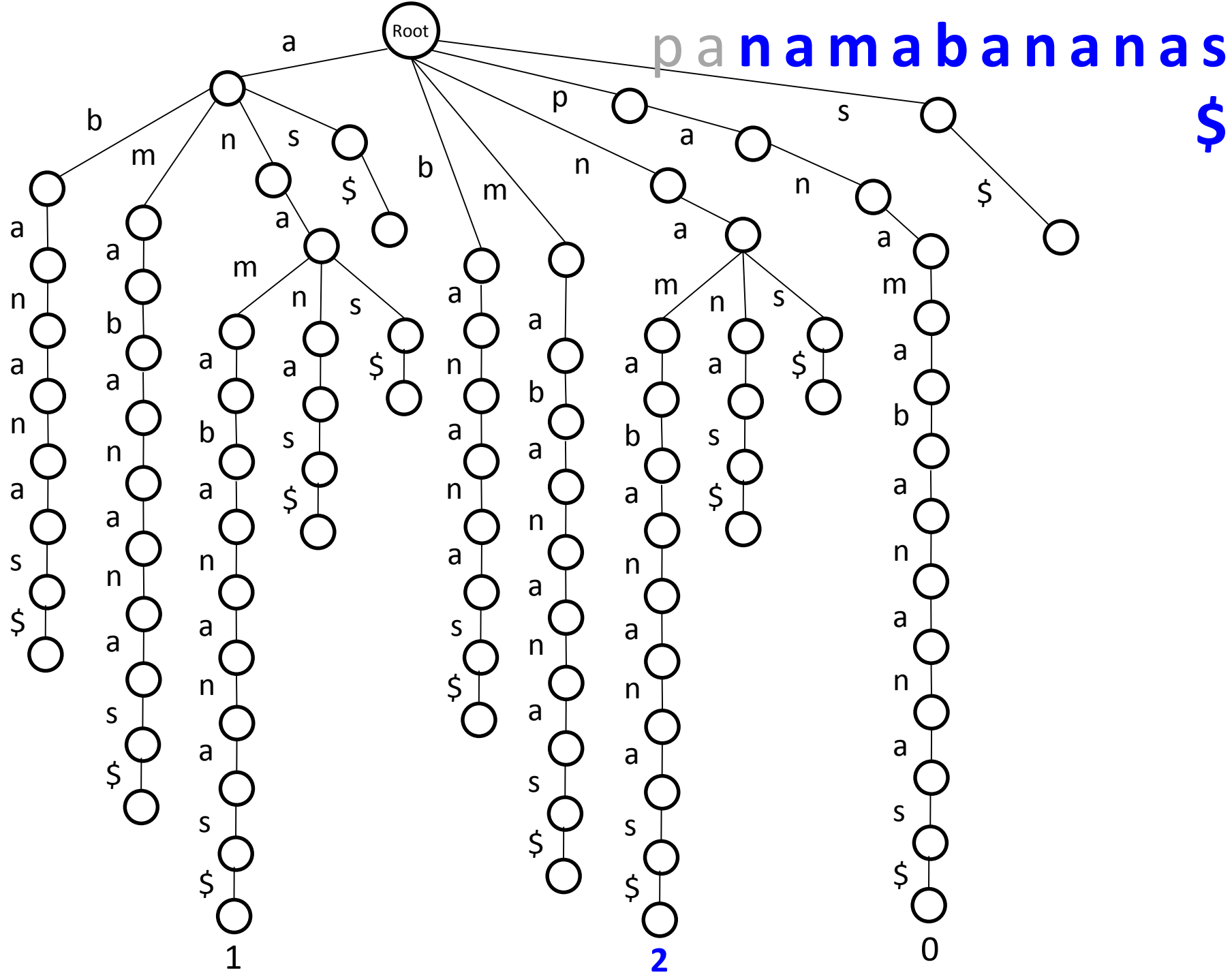


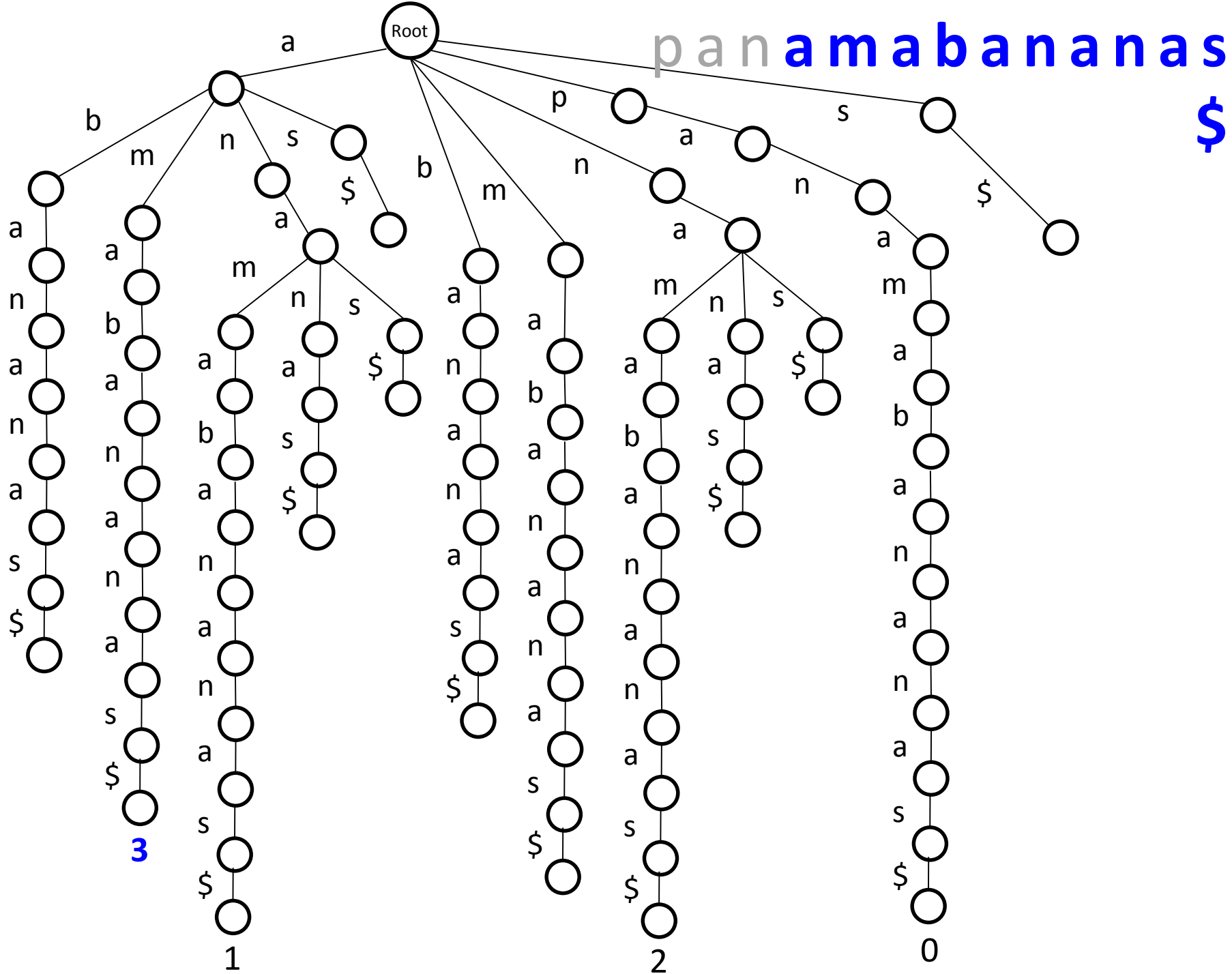
panamabanas\$

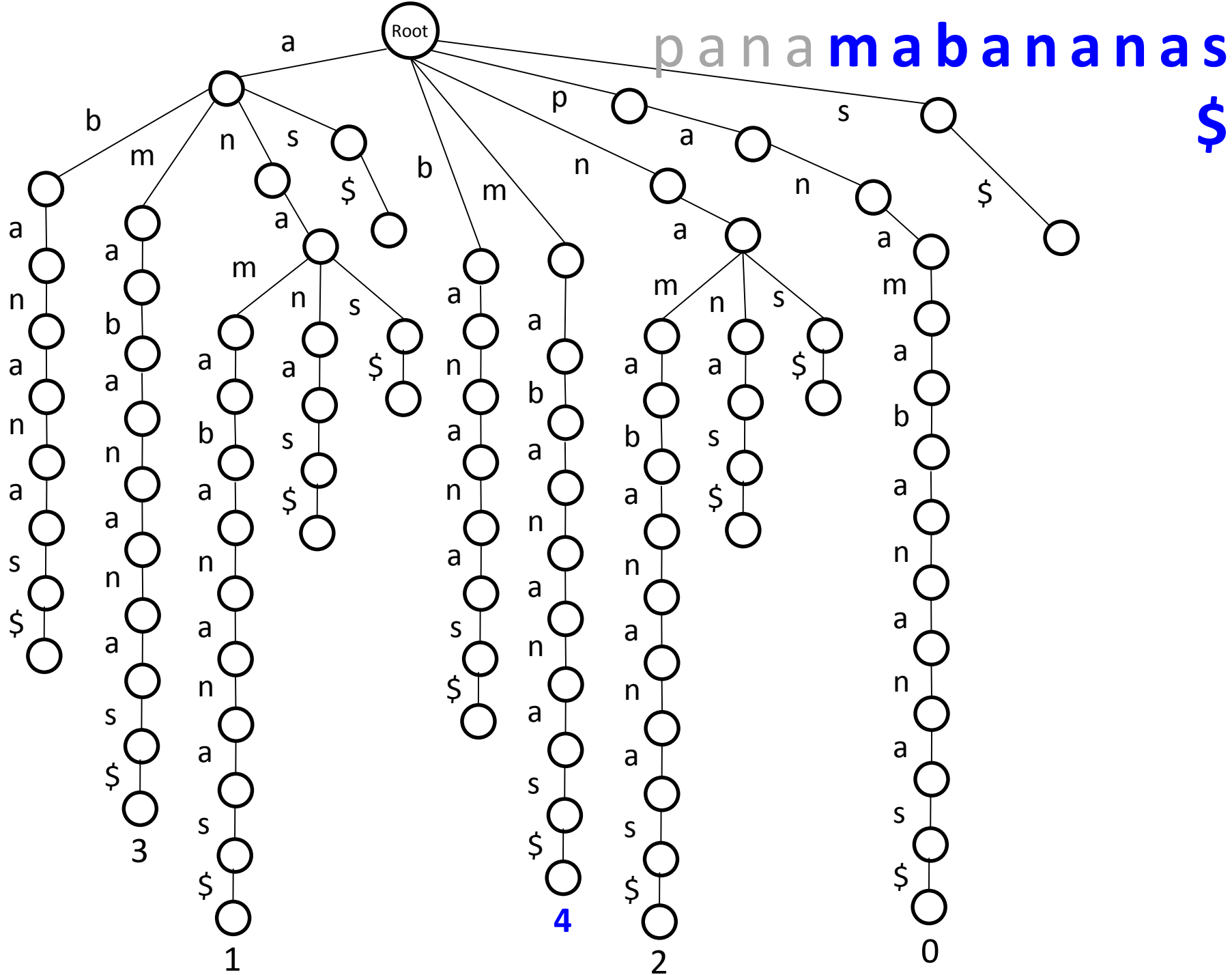


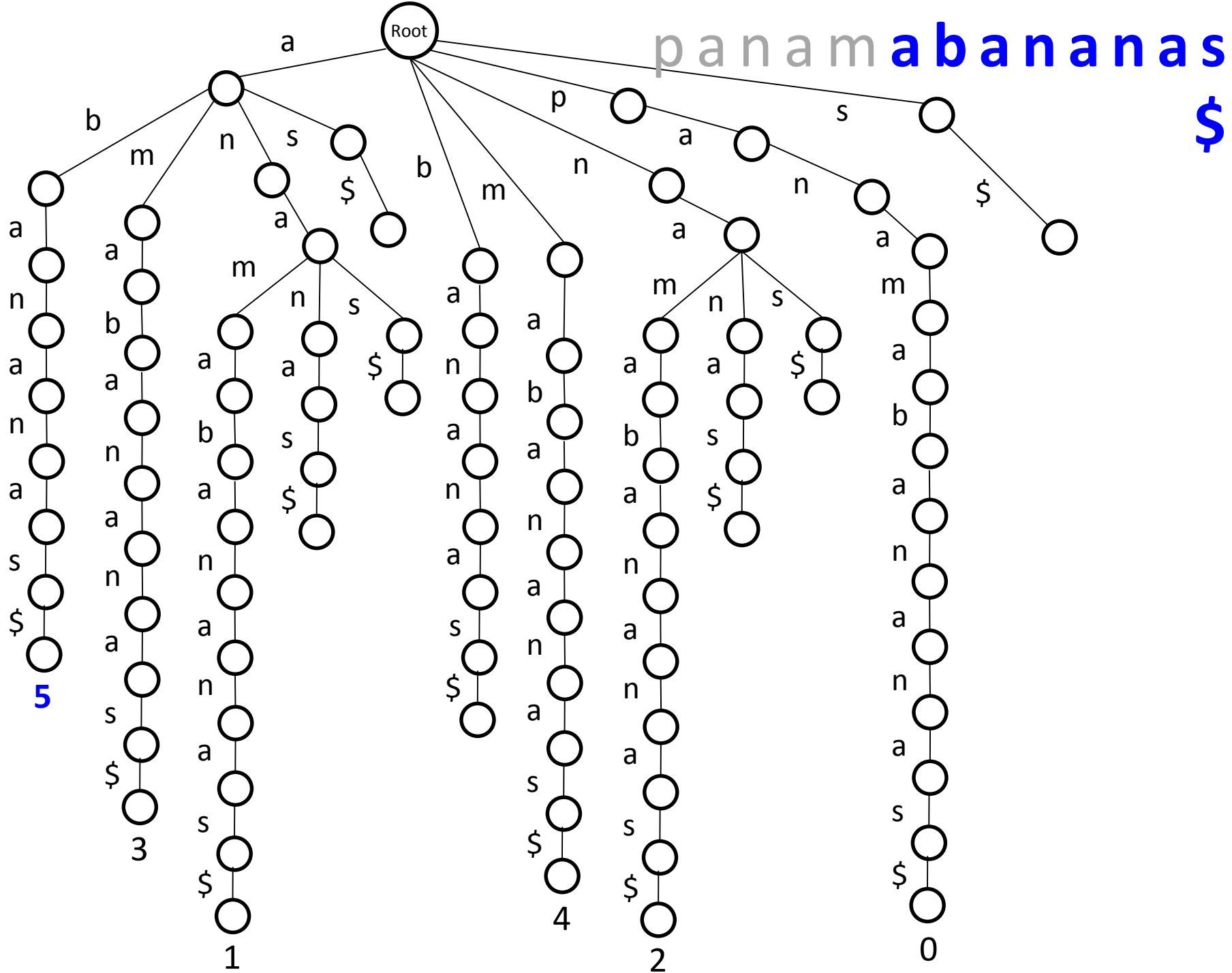
panamabanas\$



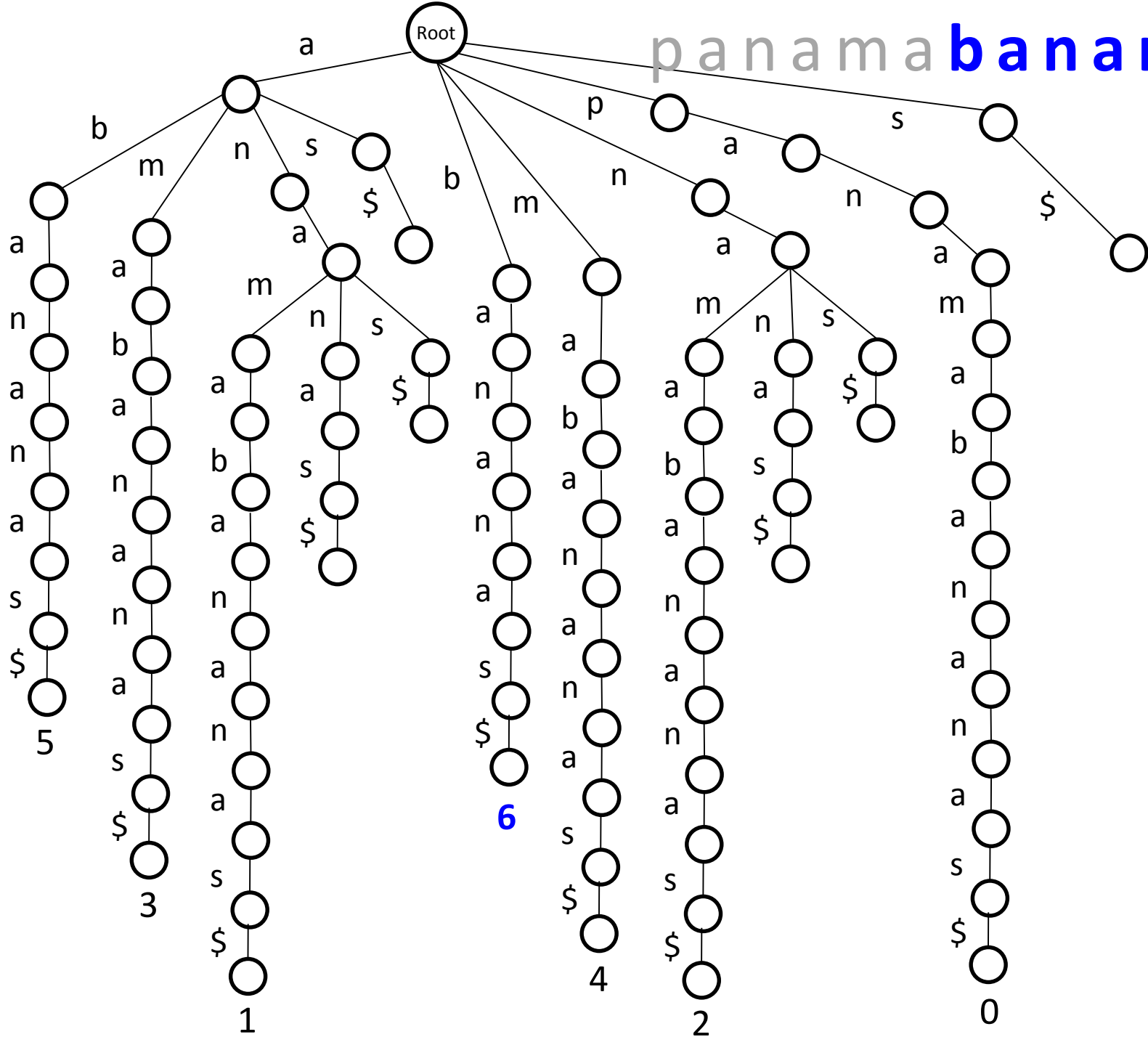




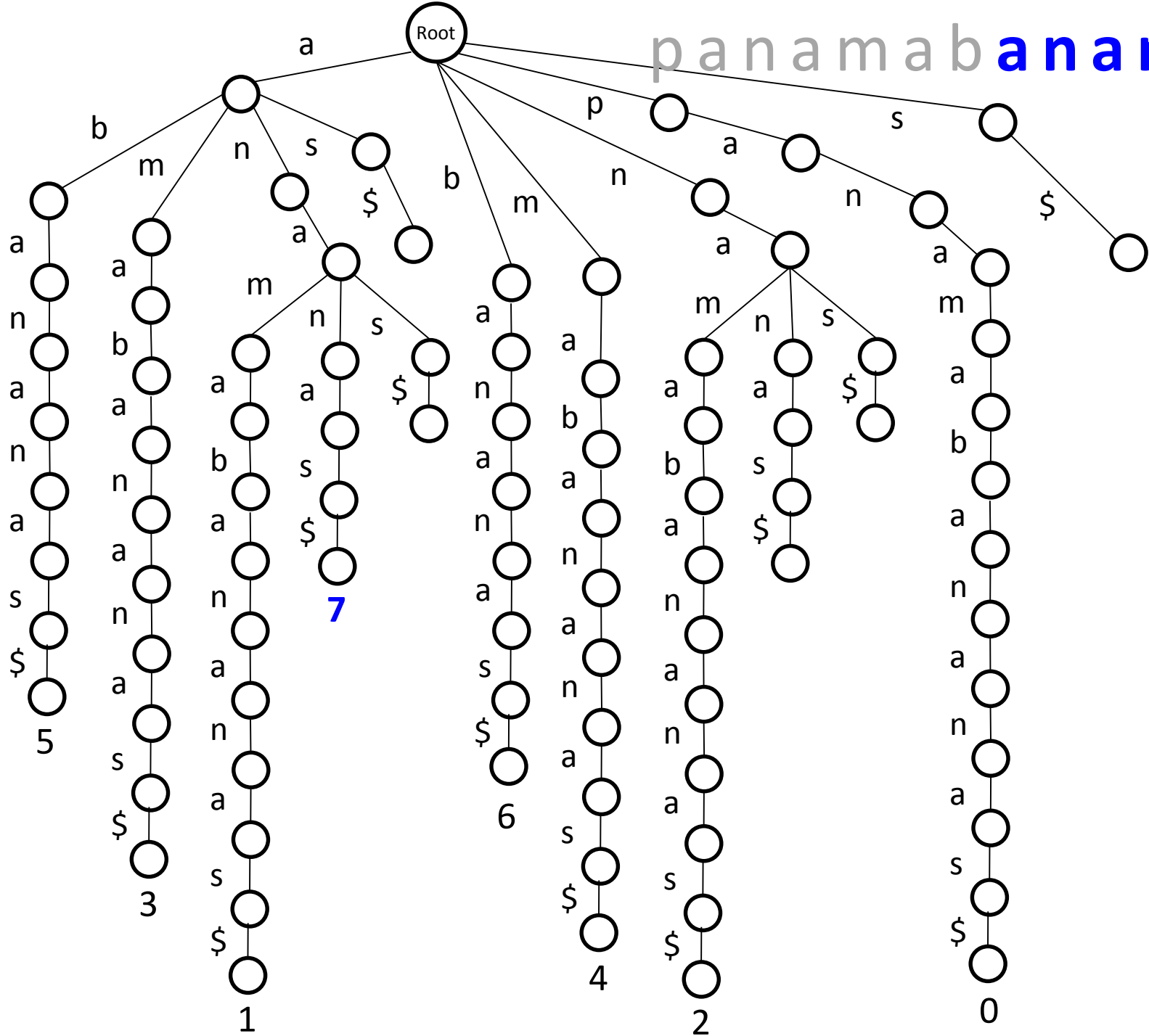




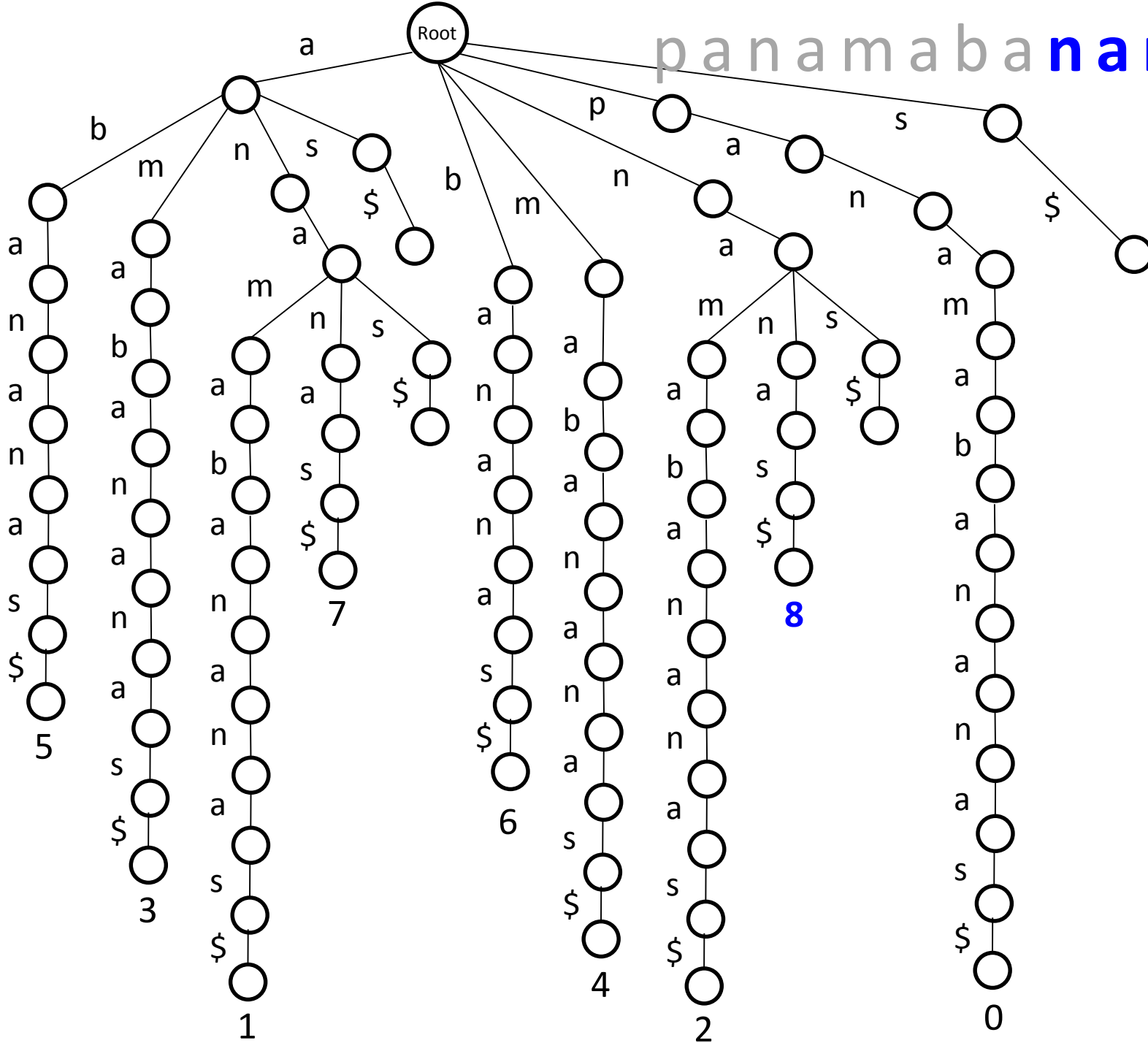
panama **bananas\$**



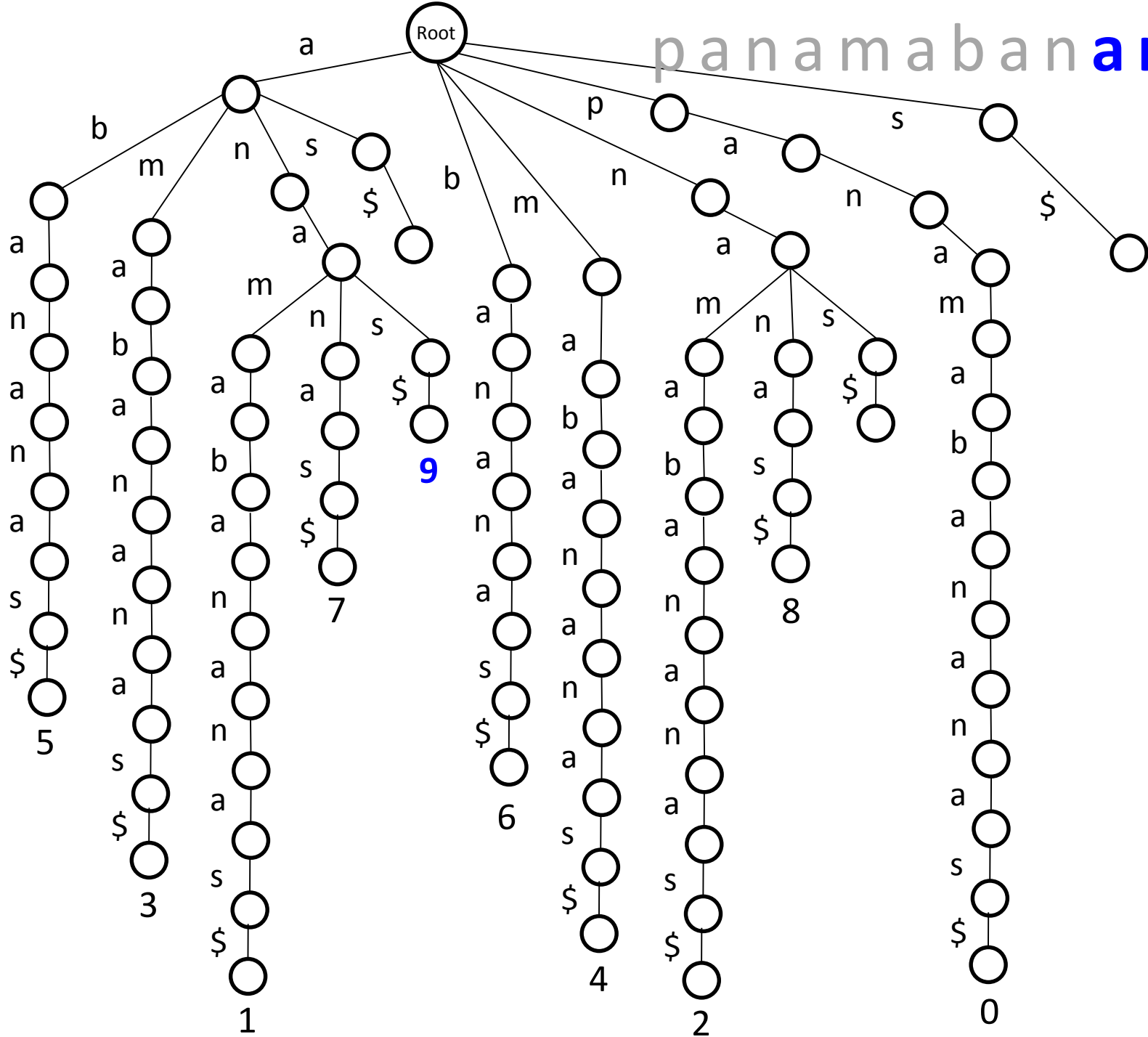
panama bananas\$



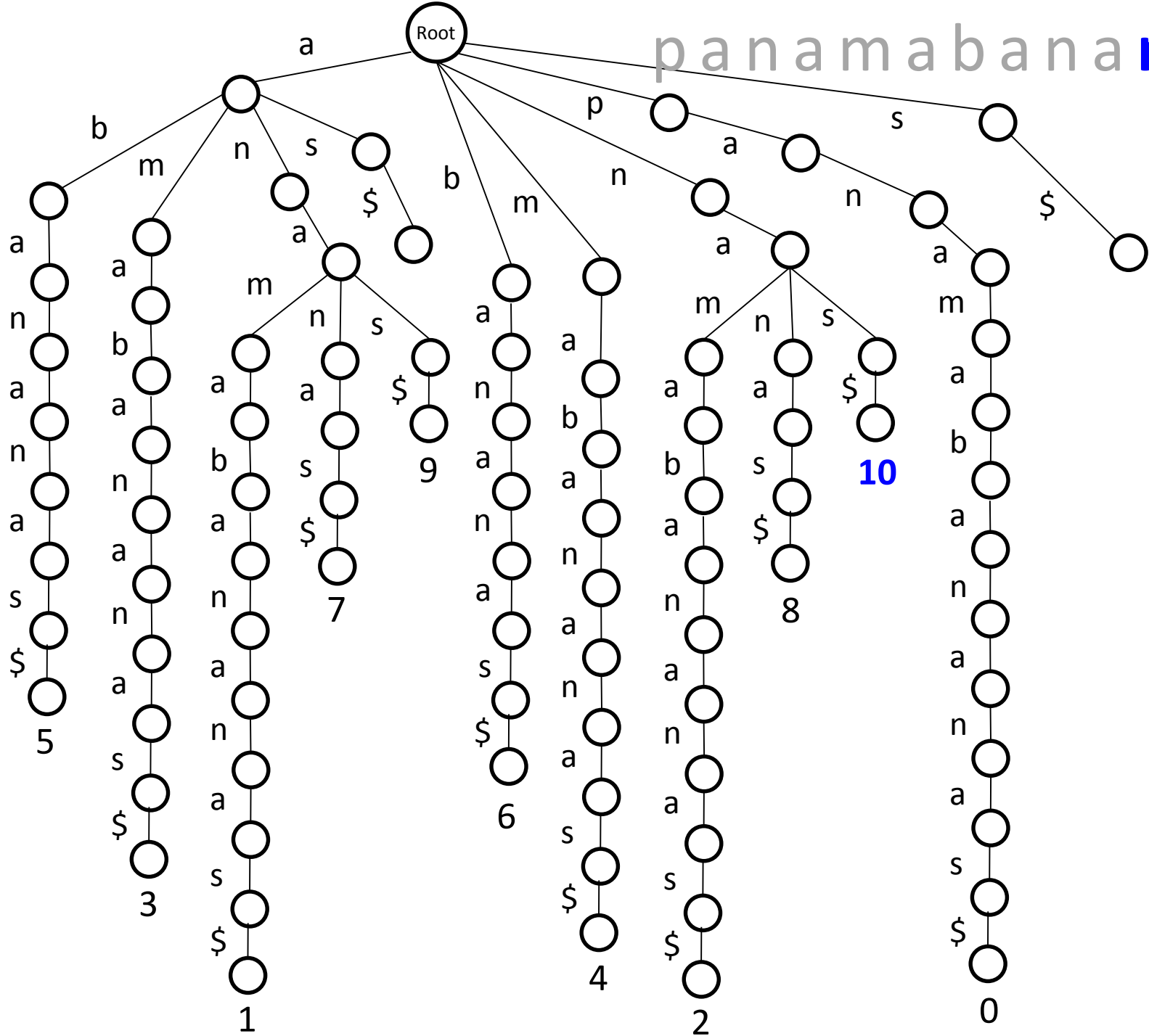
panama **bananas** \$



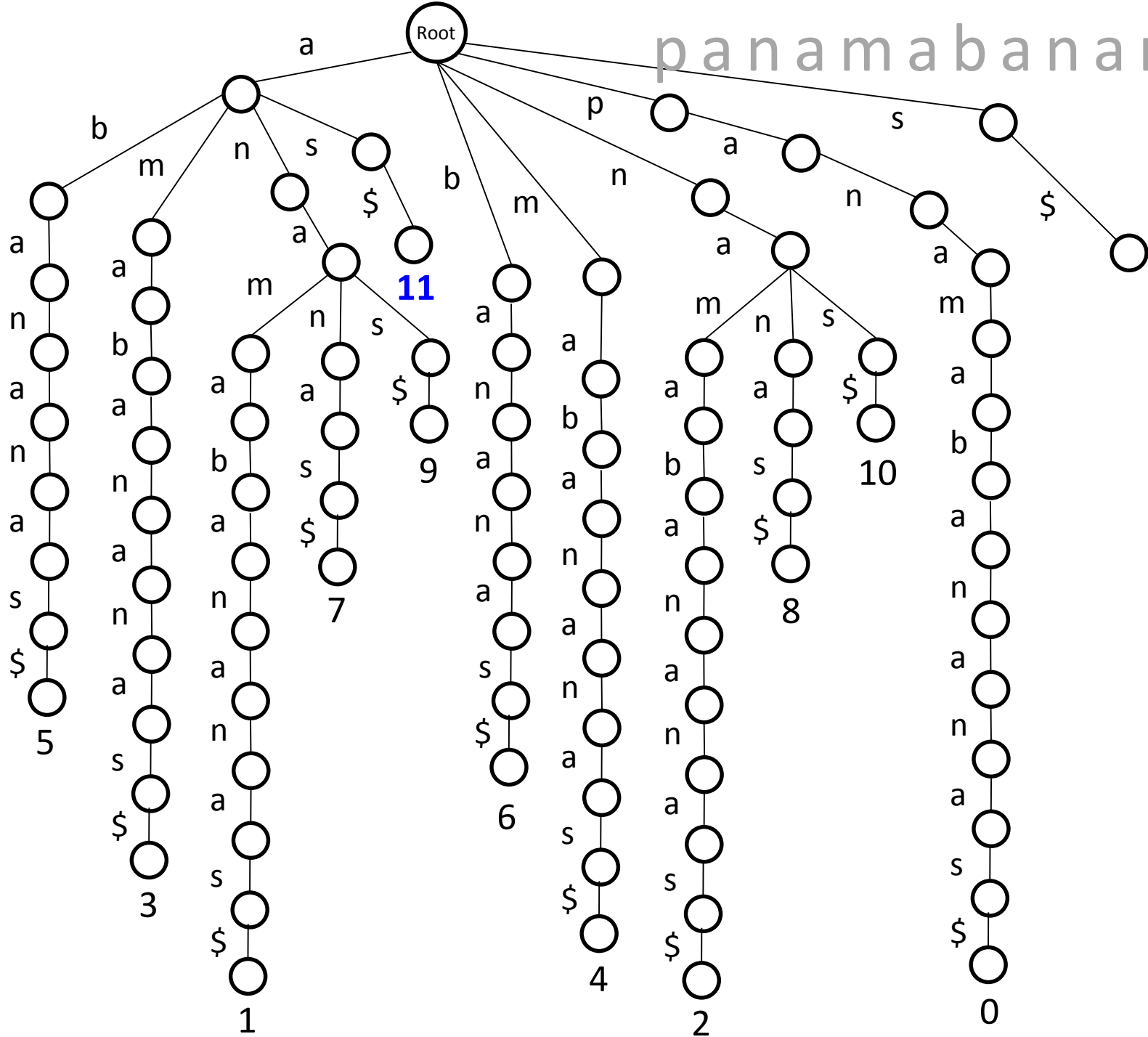
panama bananas\$

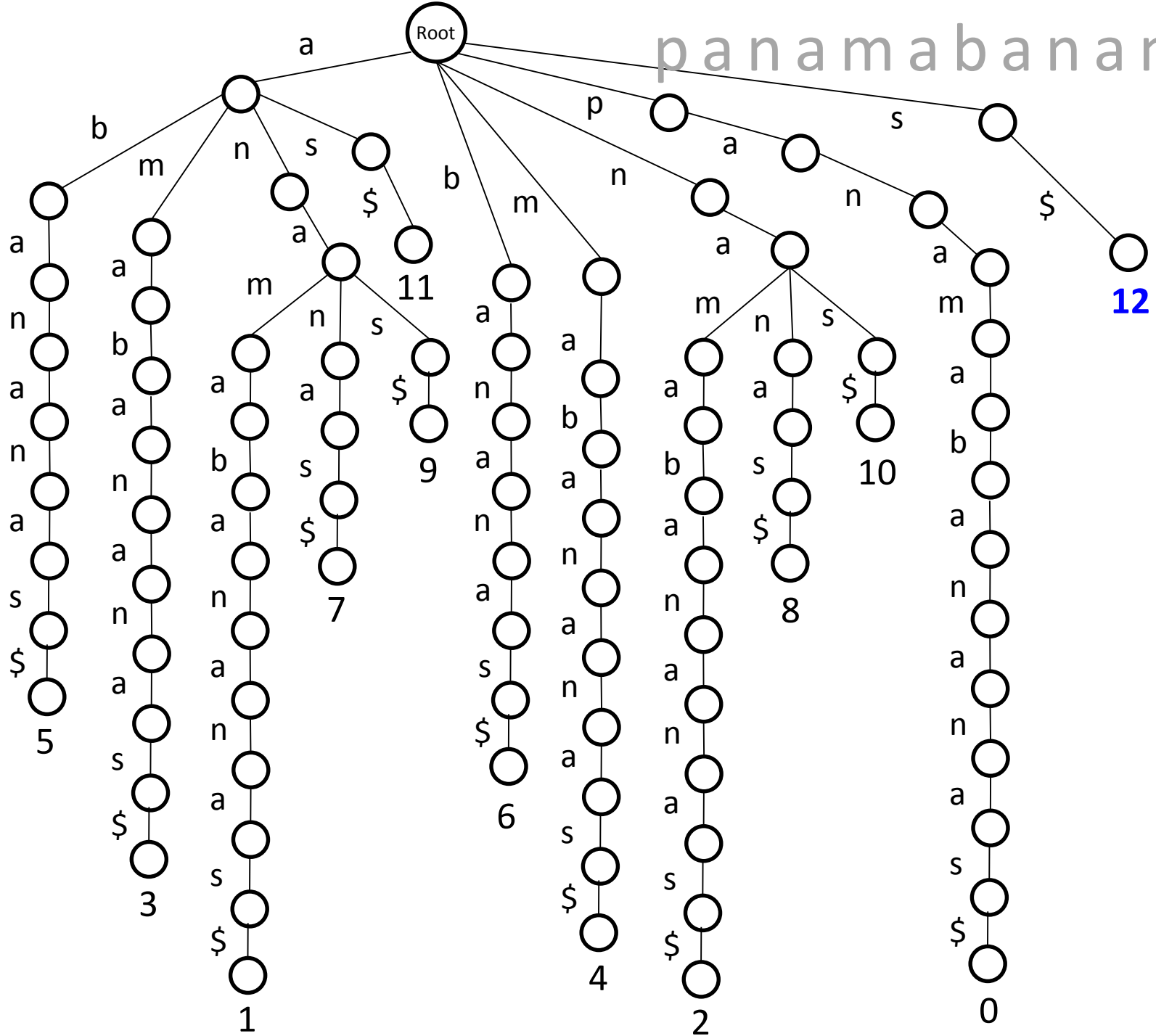


panamabananas\$



panamabananas\$



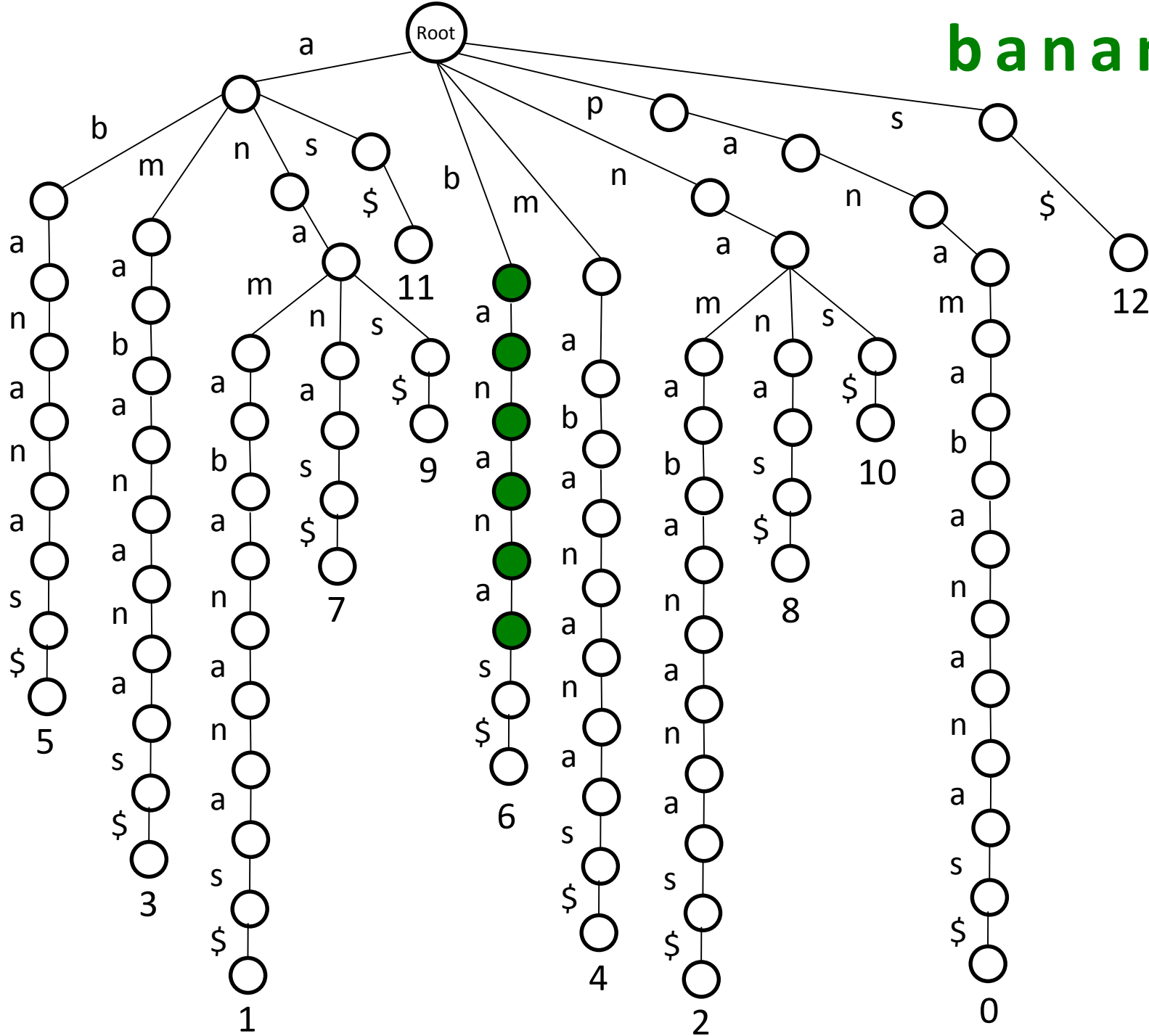


panamabananas\$

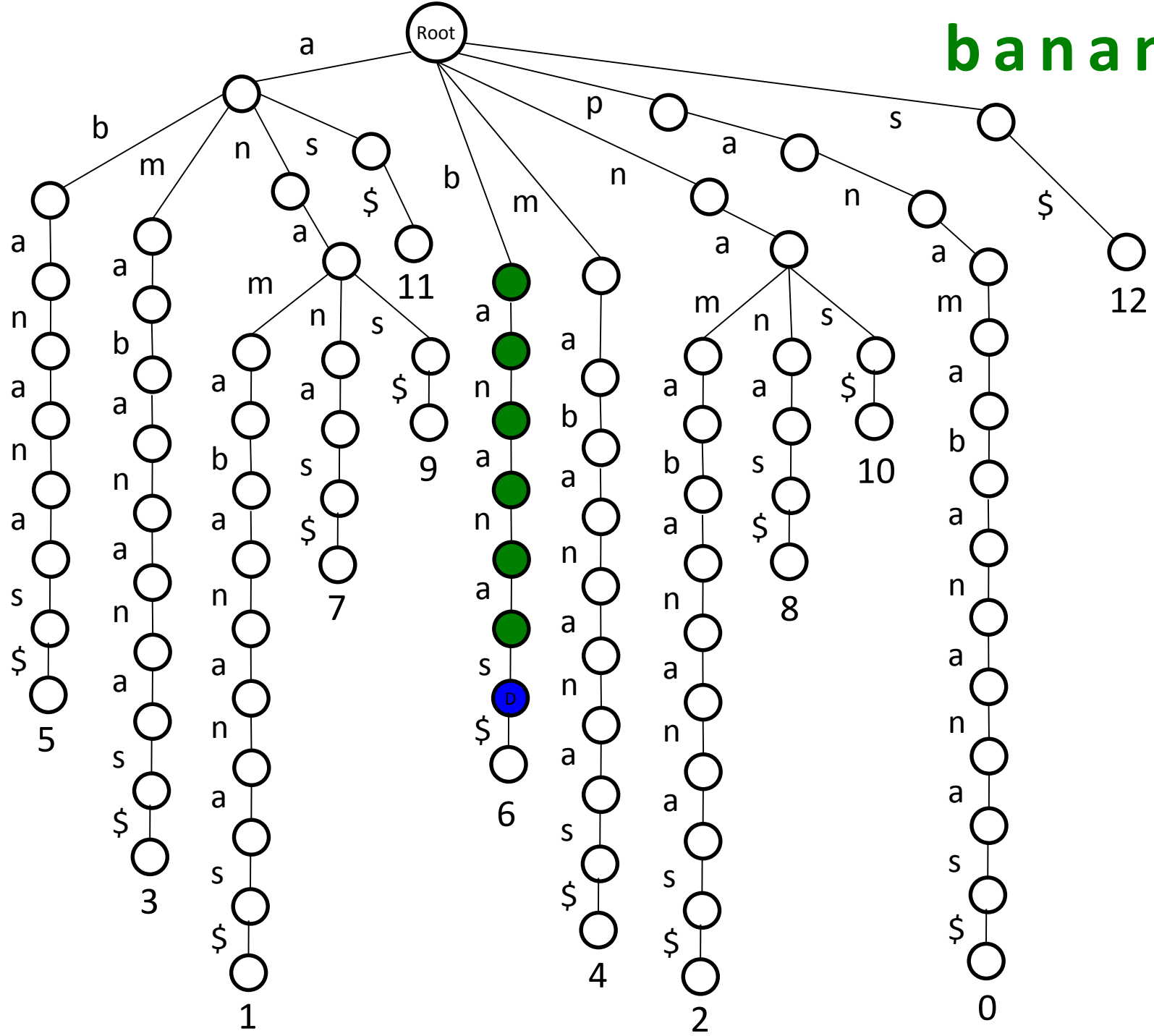
Walking Down to the Leaves to Find Matches

- Once we find a match, we “walk down” to the leaf (or leaves) in order to find the starting position of the match.

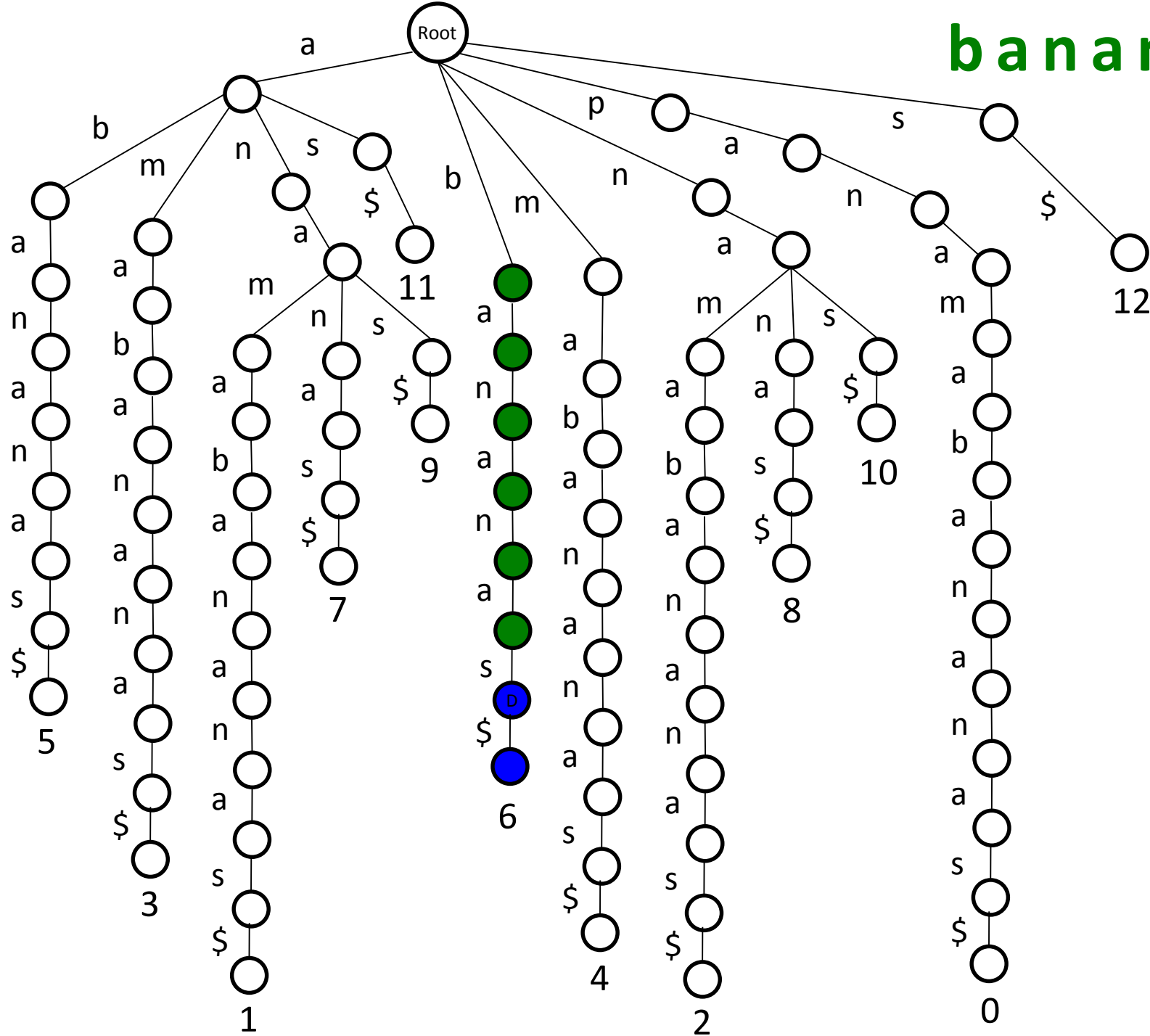
banana

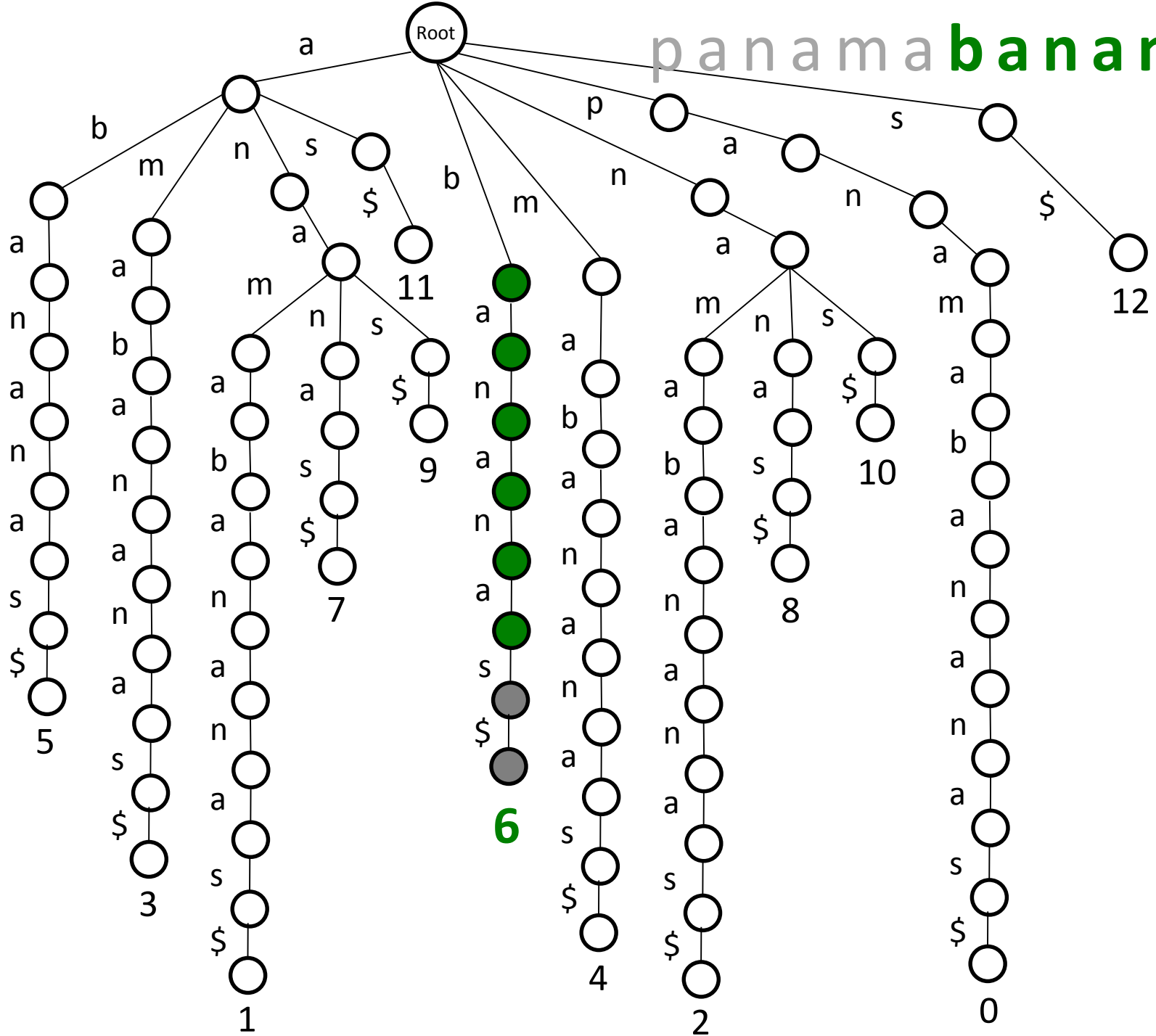


banana



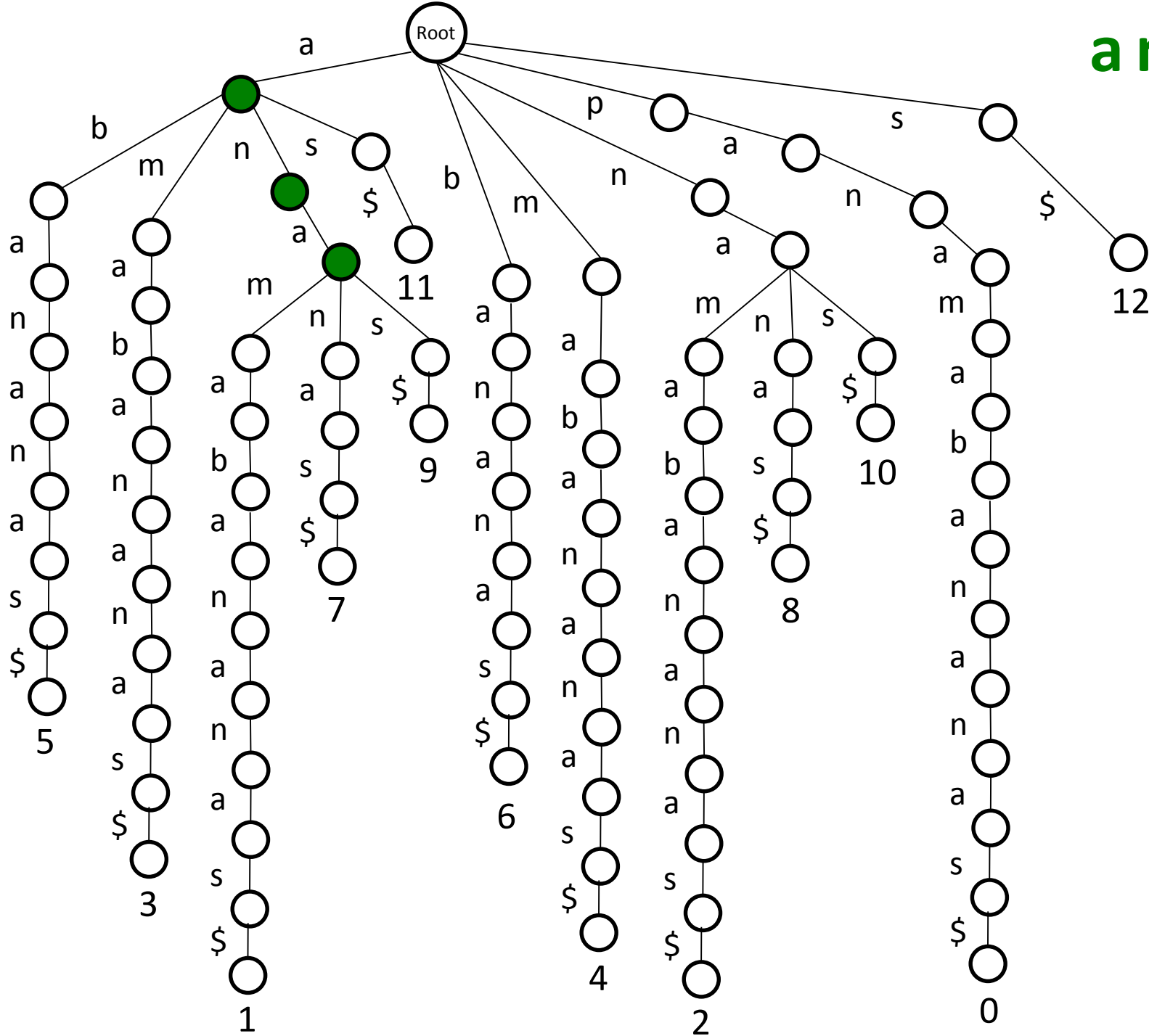
banana



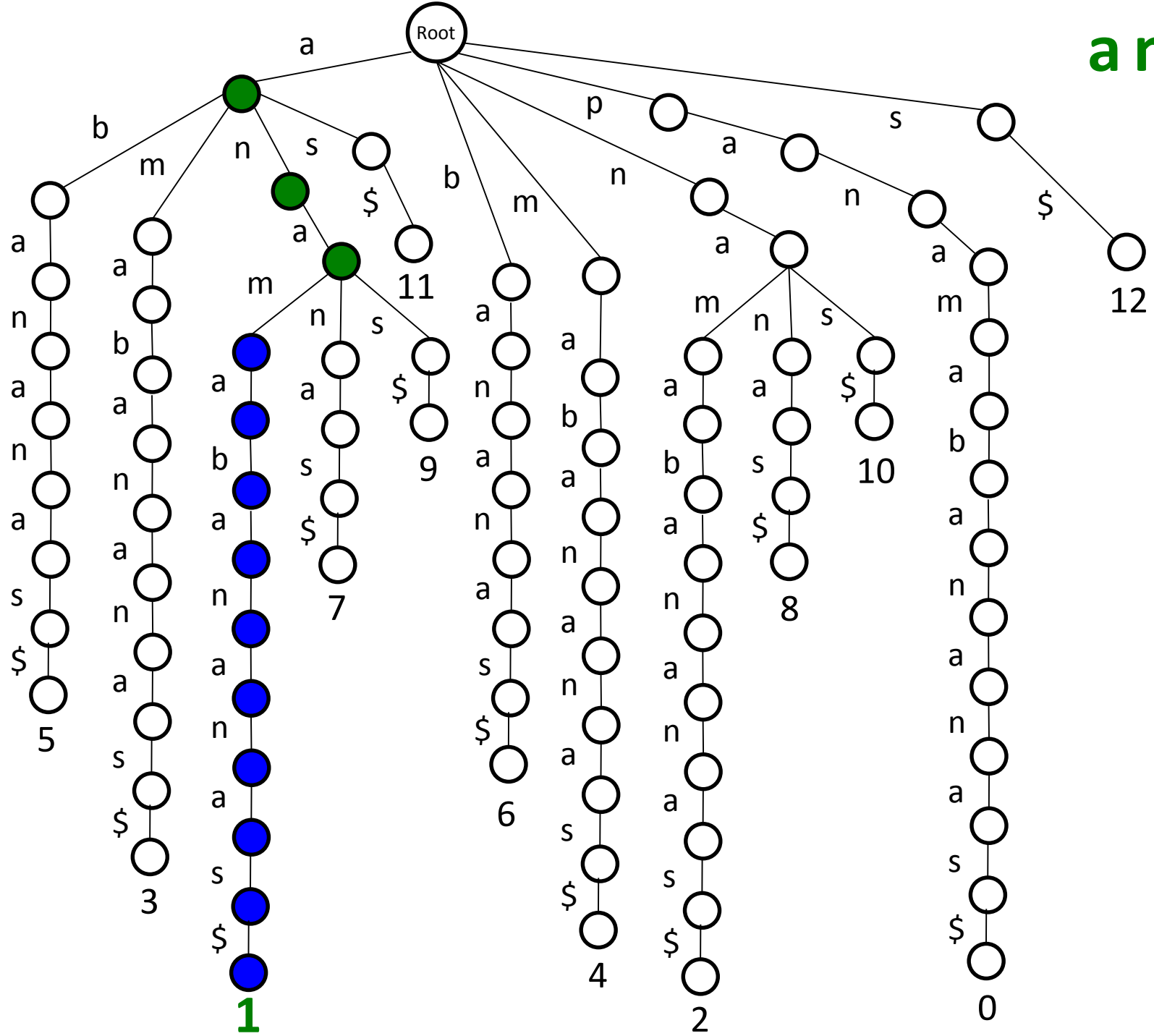


panama **bananas** \$

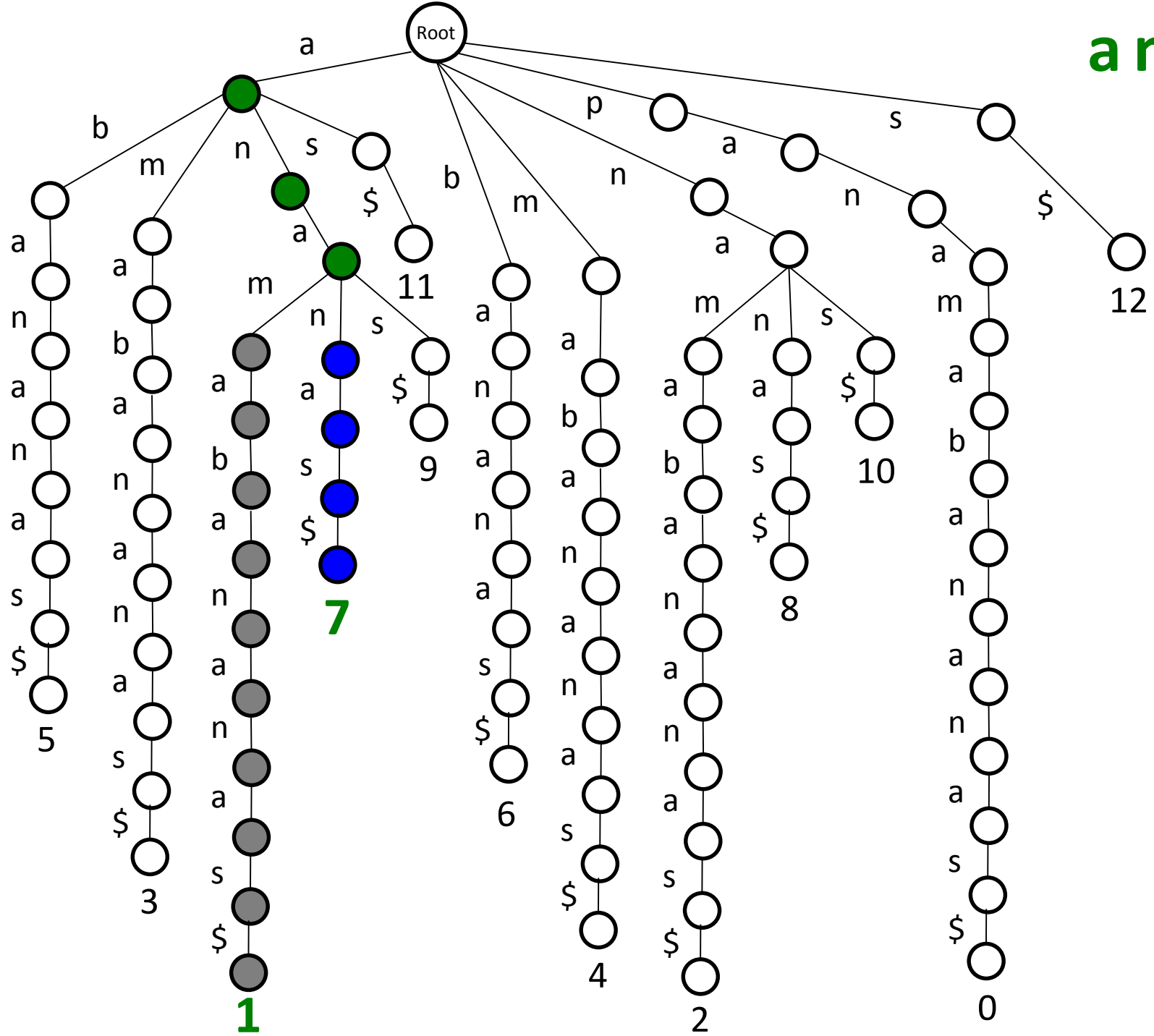
ana



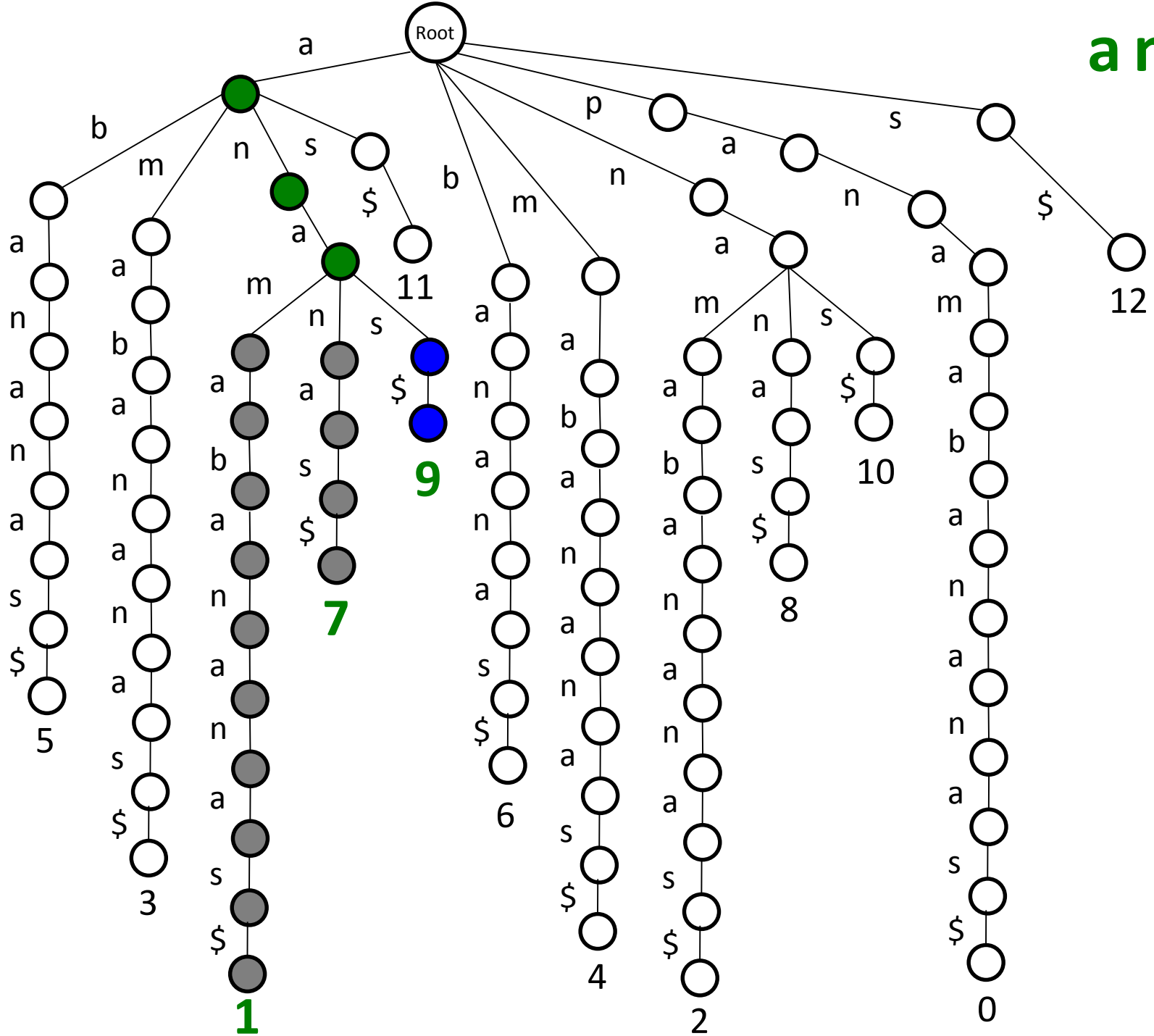
ana



ana



ana



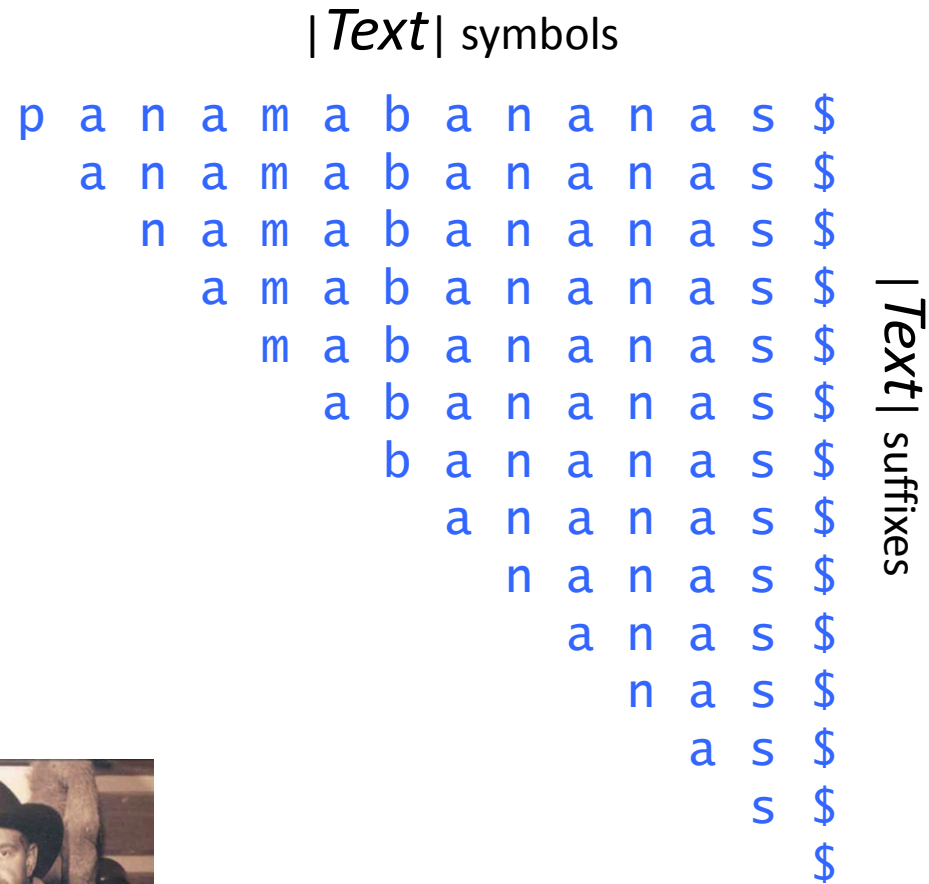
Memory Footprint of Suffix Trie

The suffix trie is formed from $|Text|$ suffixes with total length:

$$|Text| * (|Text| - 1) / 2$$

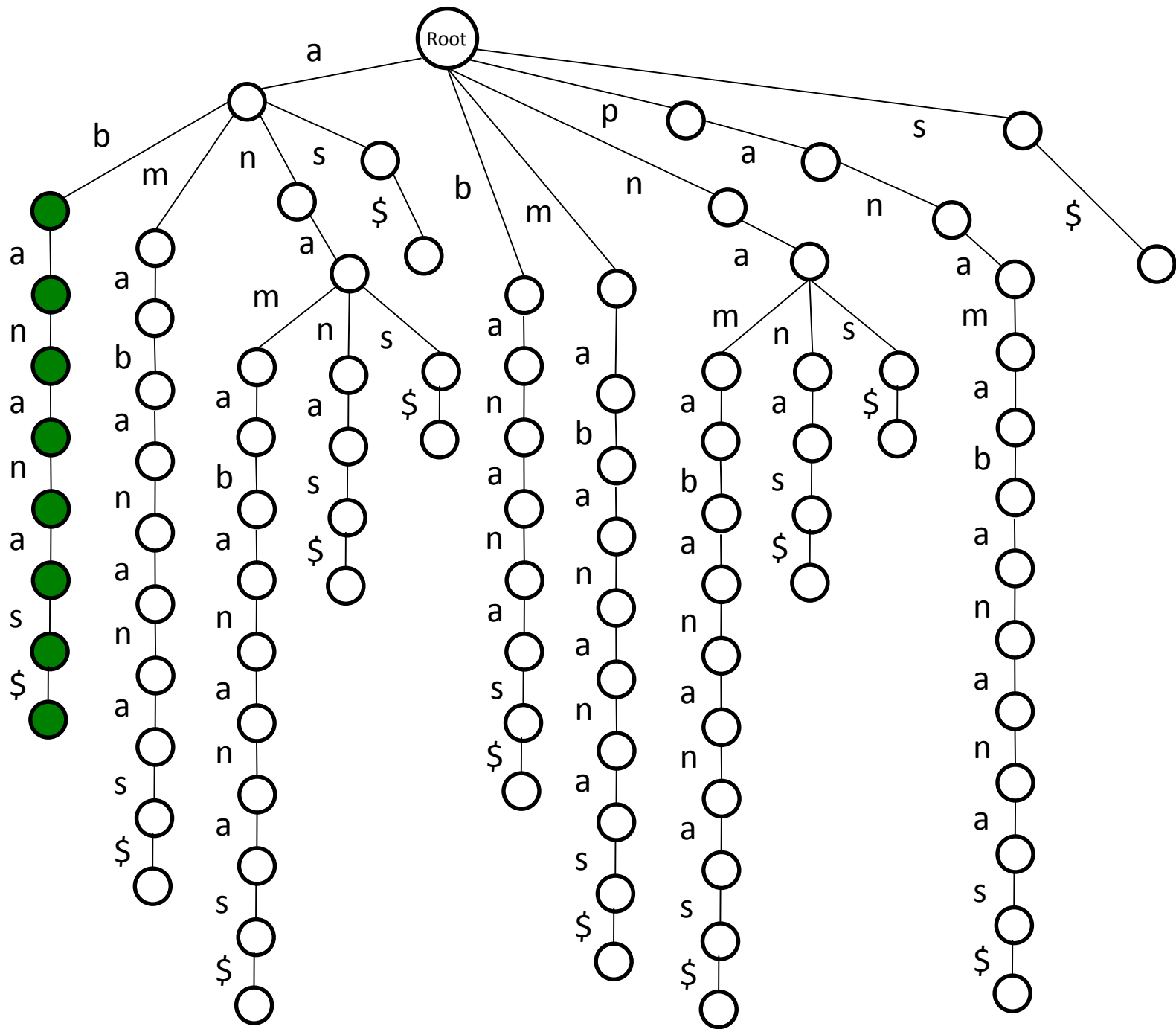
For human genome:

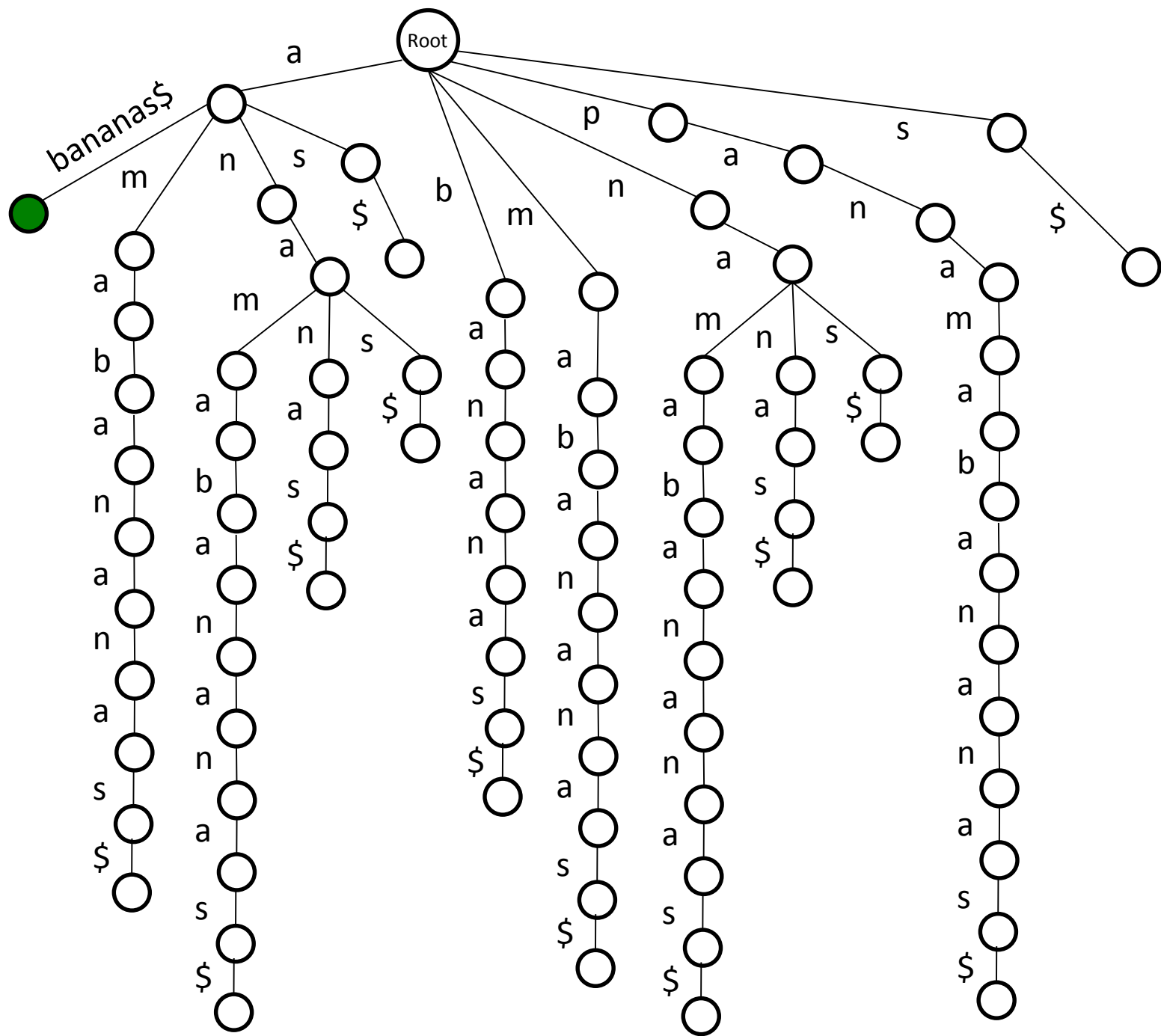
- $|Text| \approx 3 * 10^9$

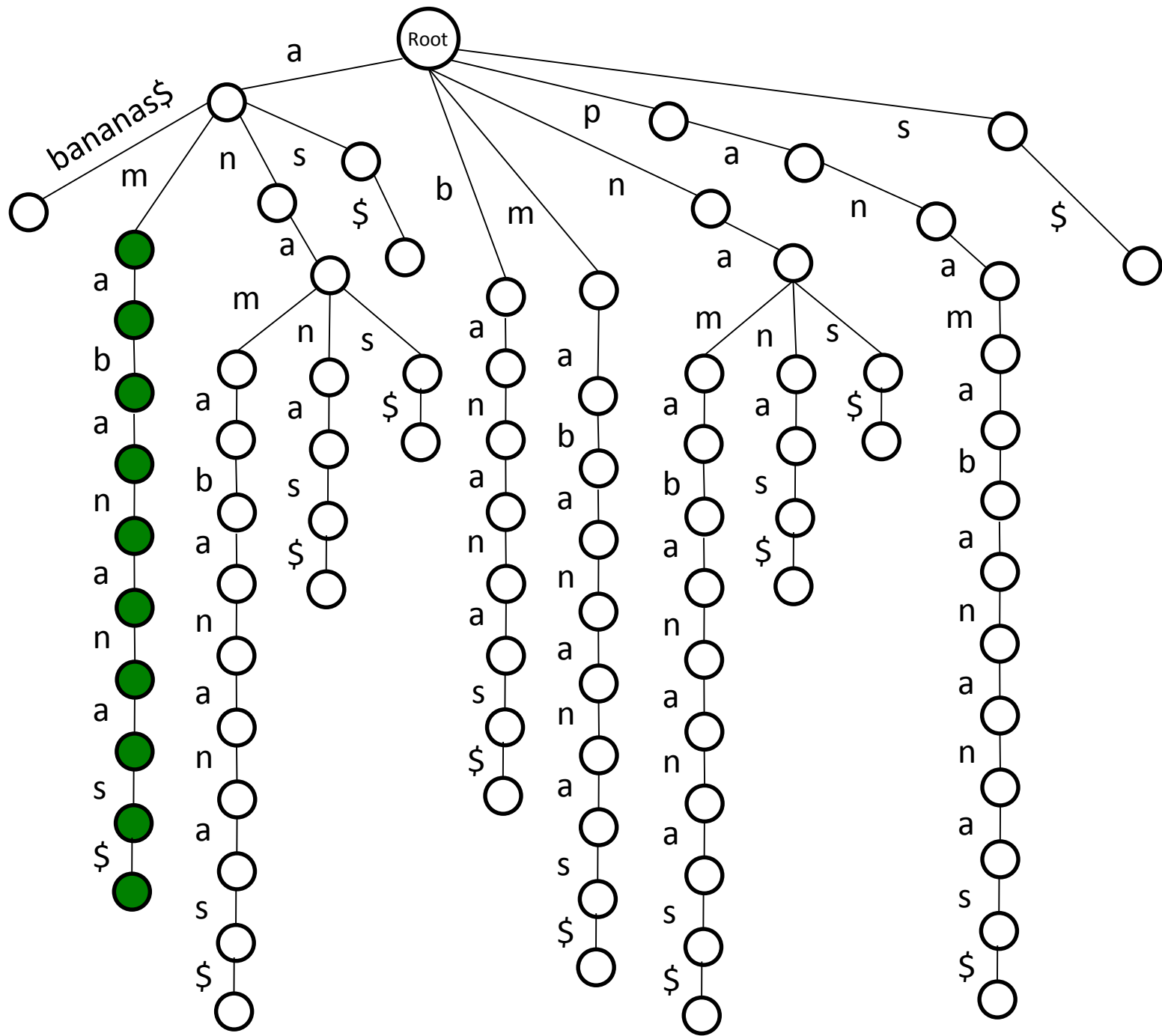


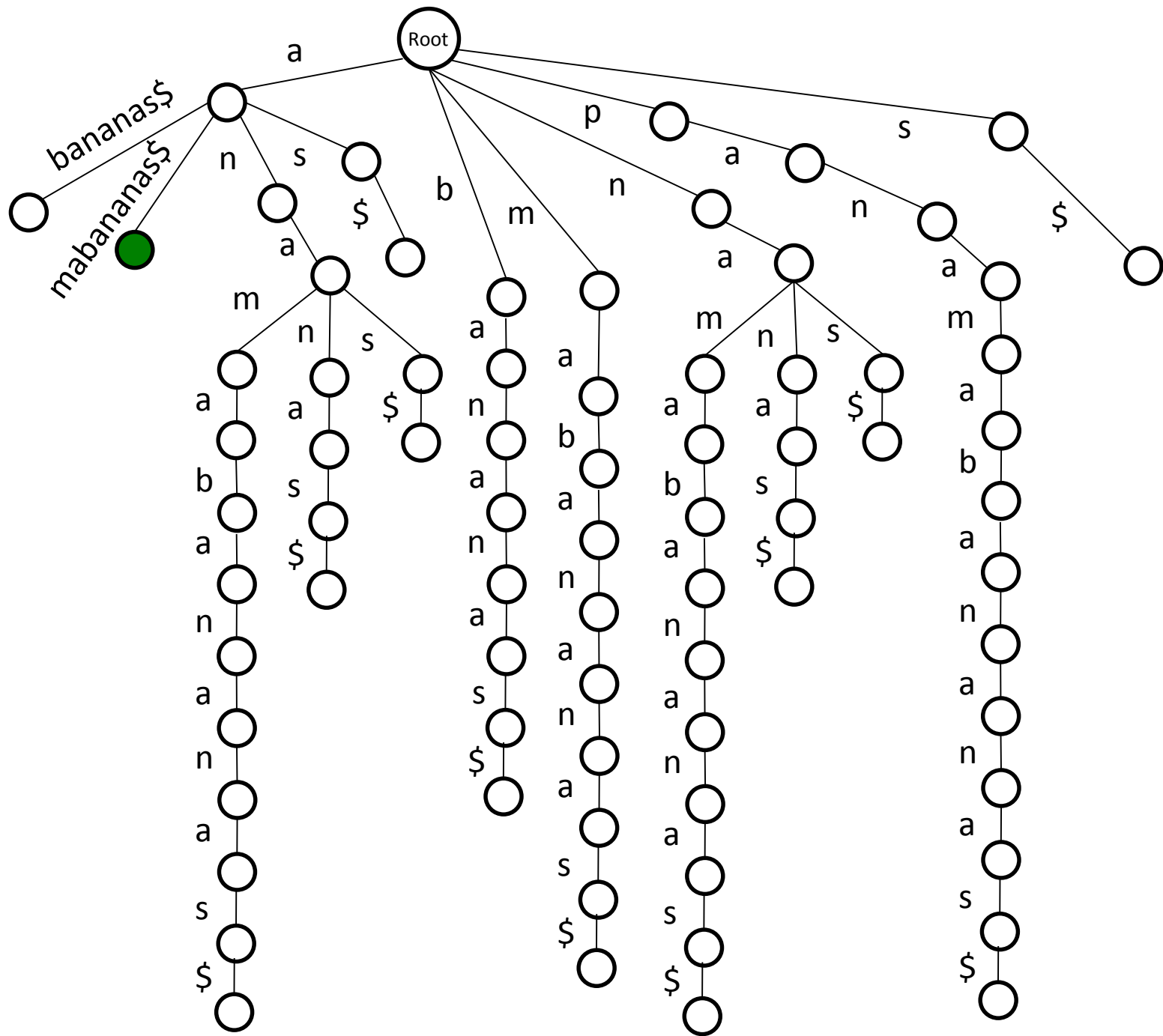
Outline

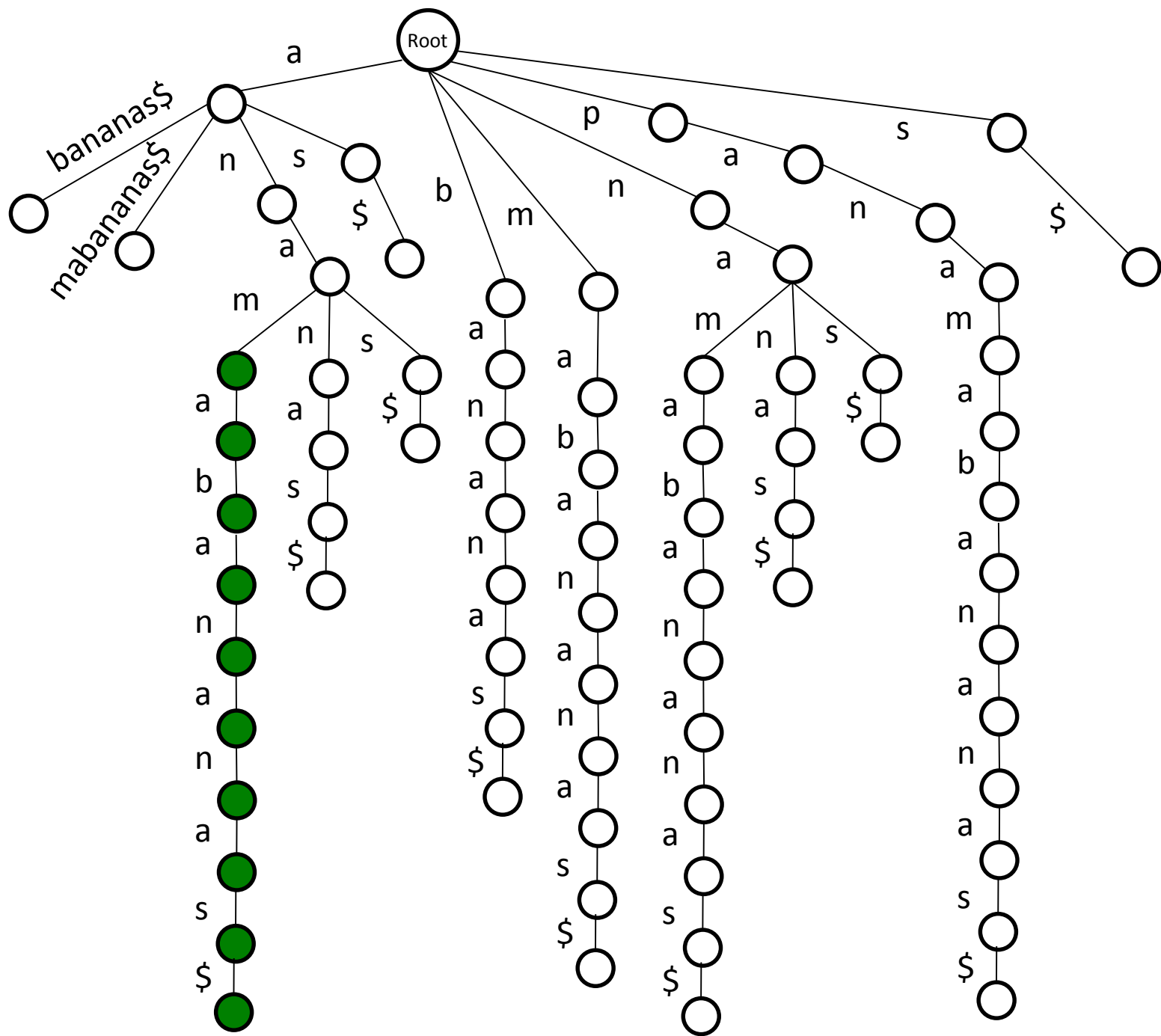
- From Genome Sequencing to Pattern Matching
- Brute Force Approach to Pattern Matching
- Herding Patterns into Trie
- Herding Text into Suffix Trie
- **From Suffix Tries to Suffix Trees**

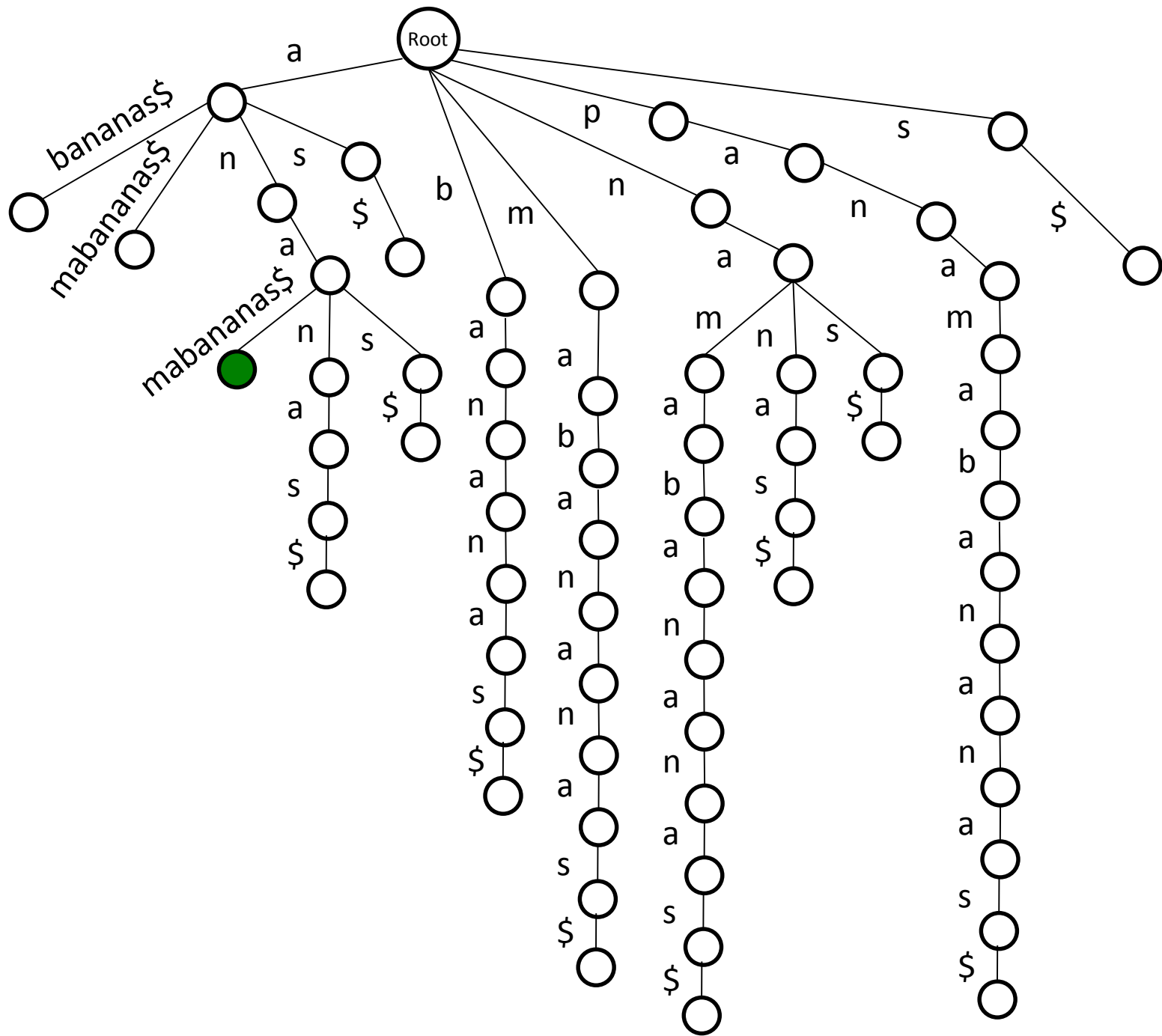


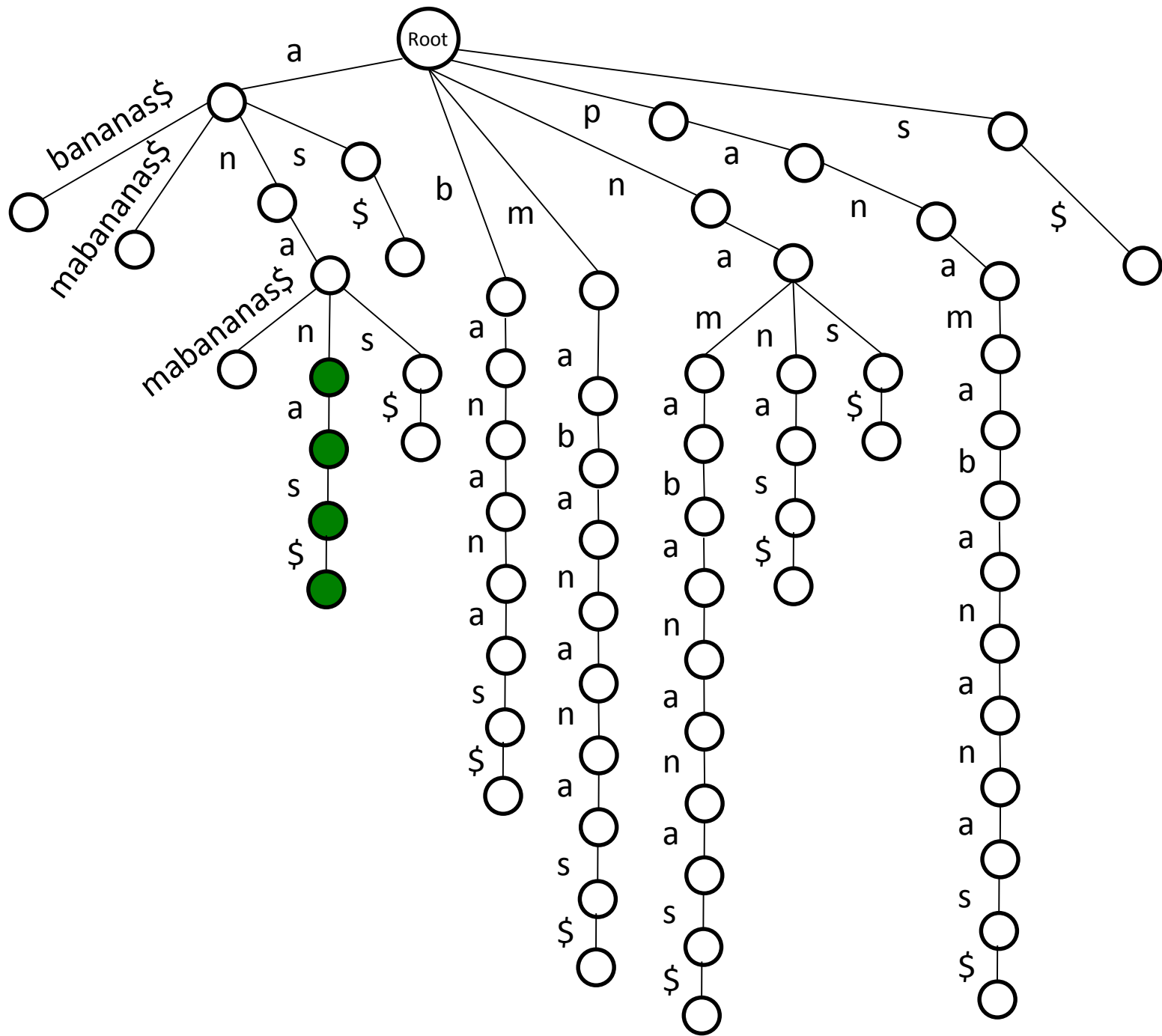


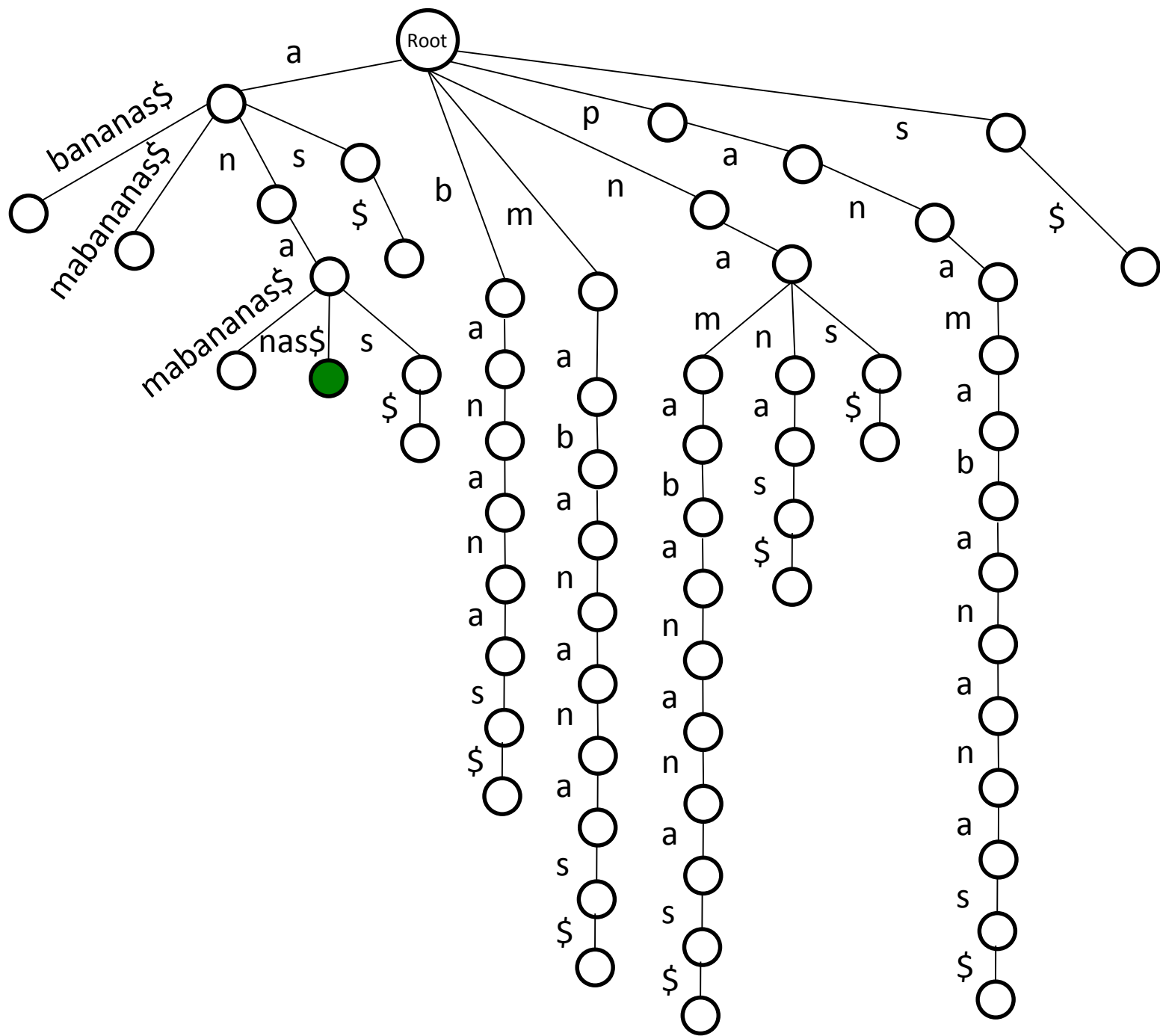


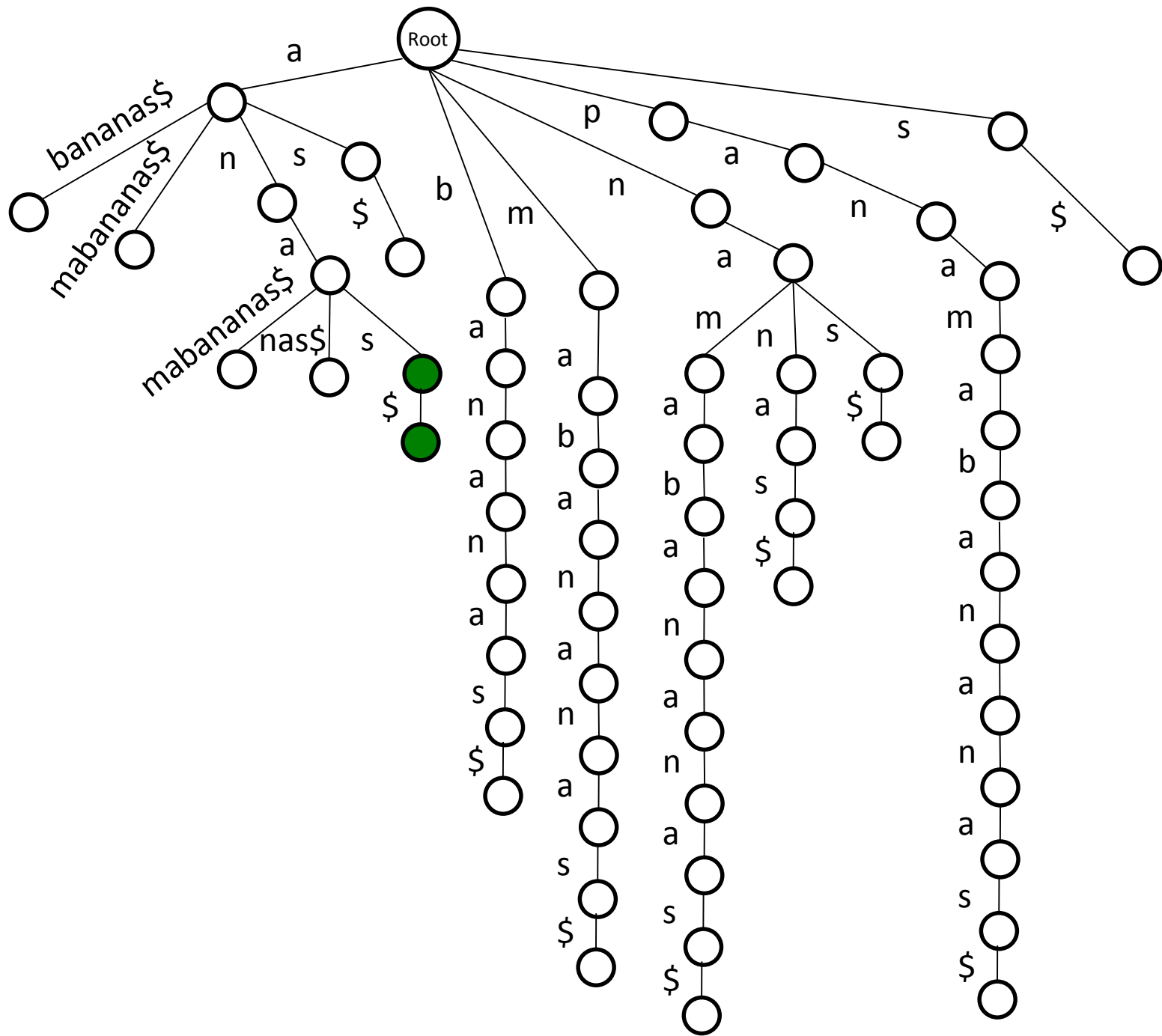


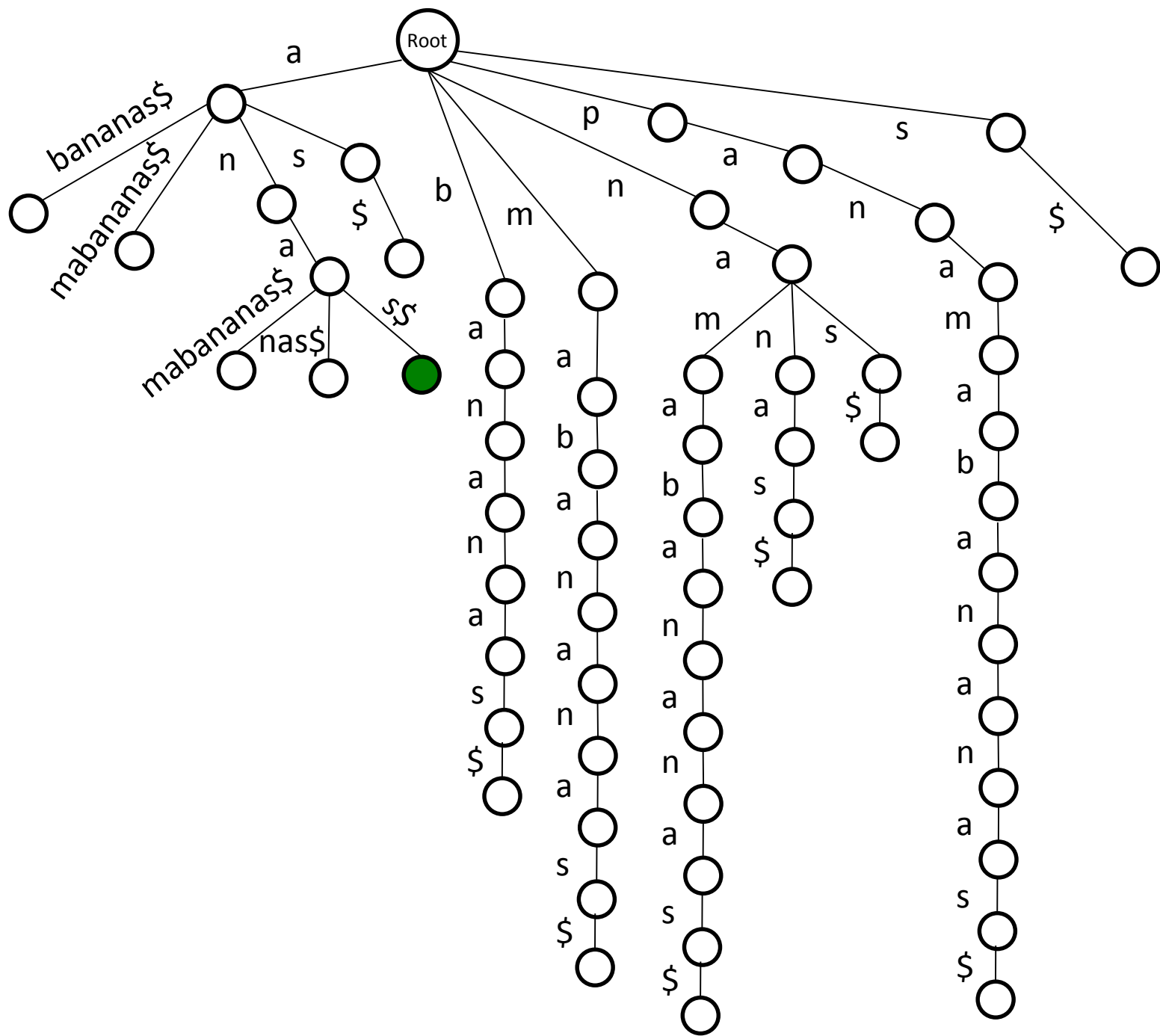


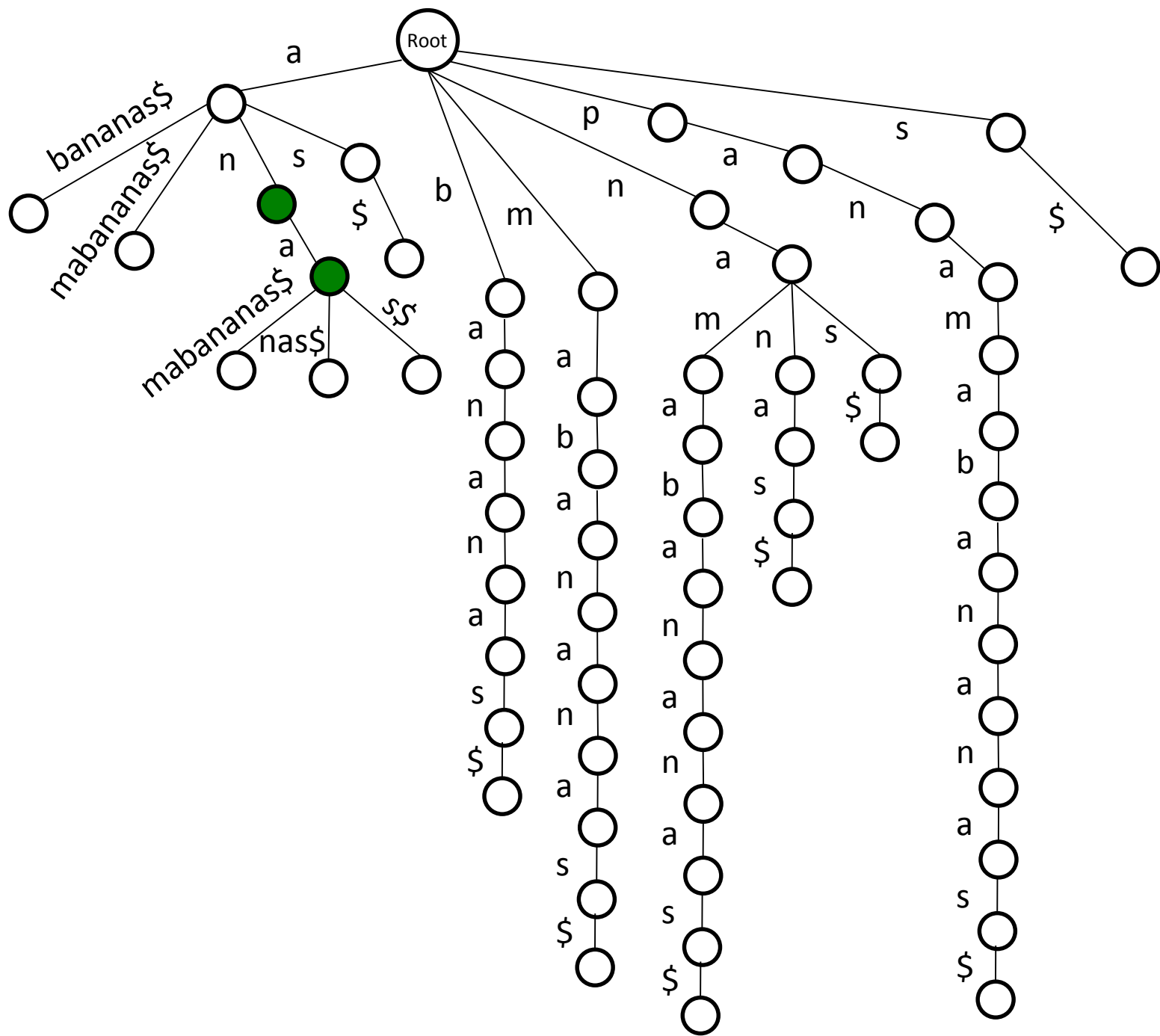


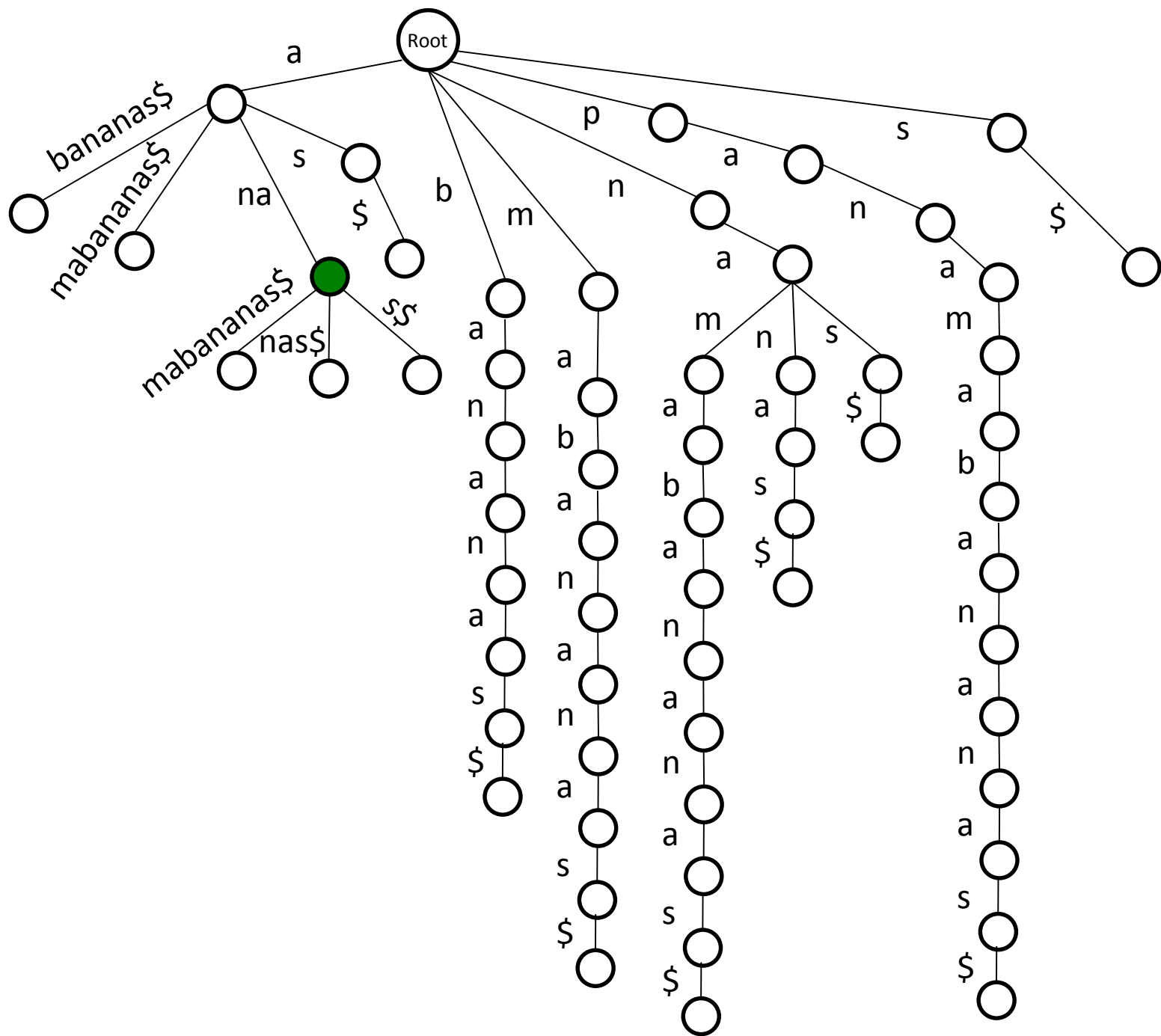


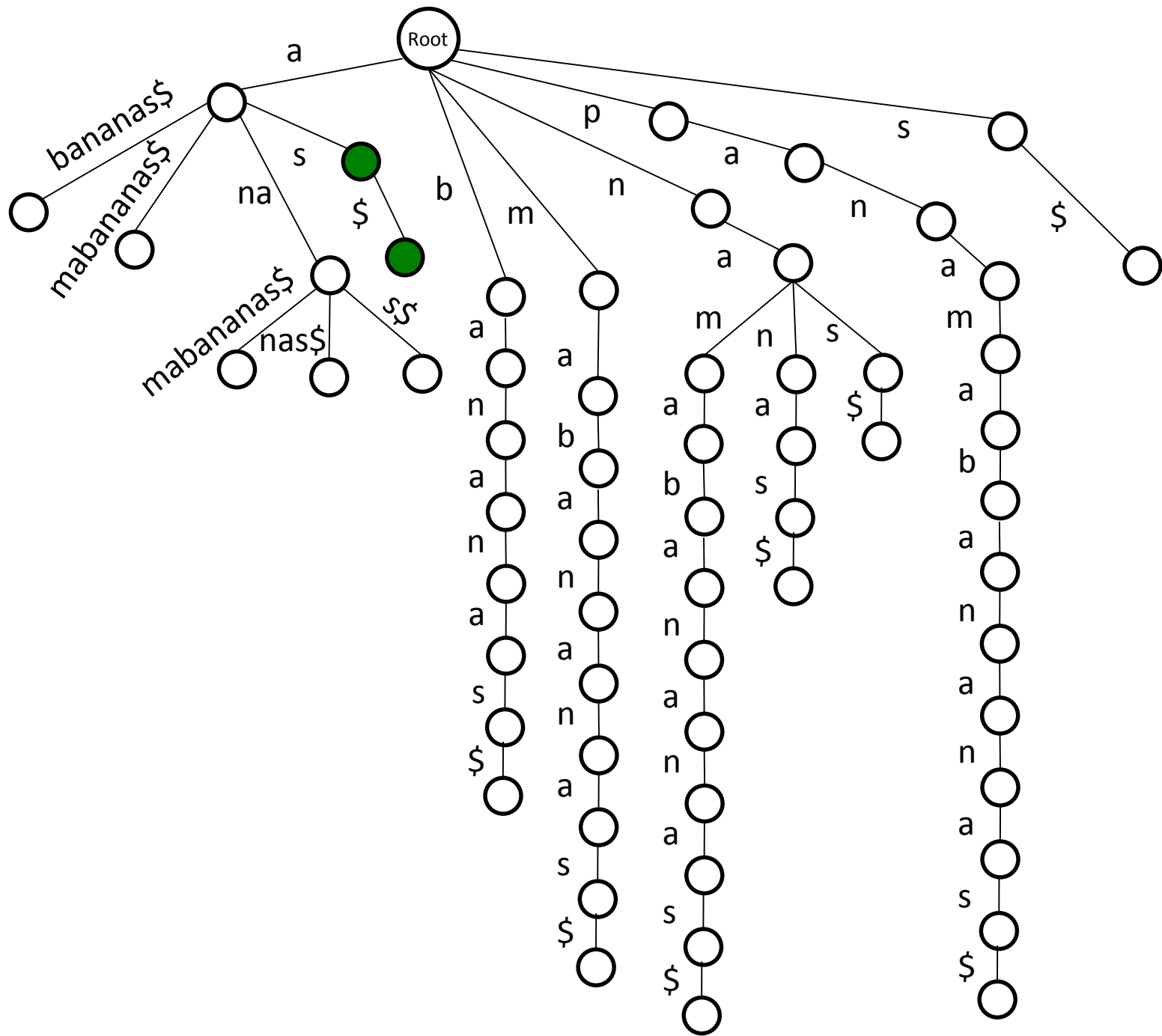


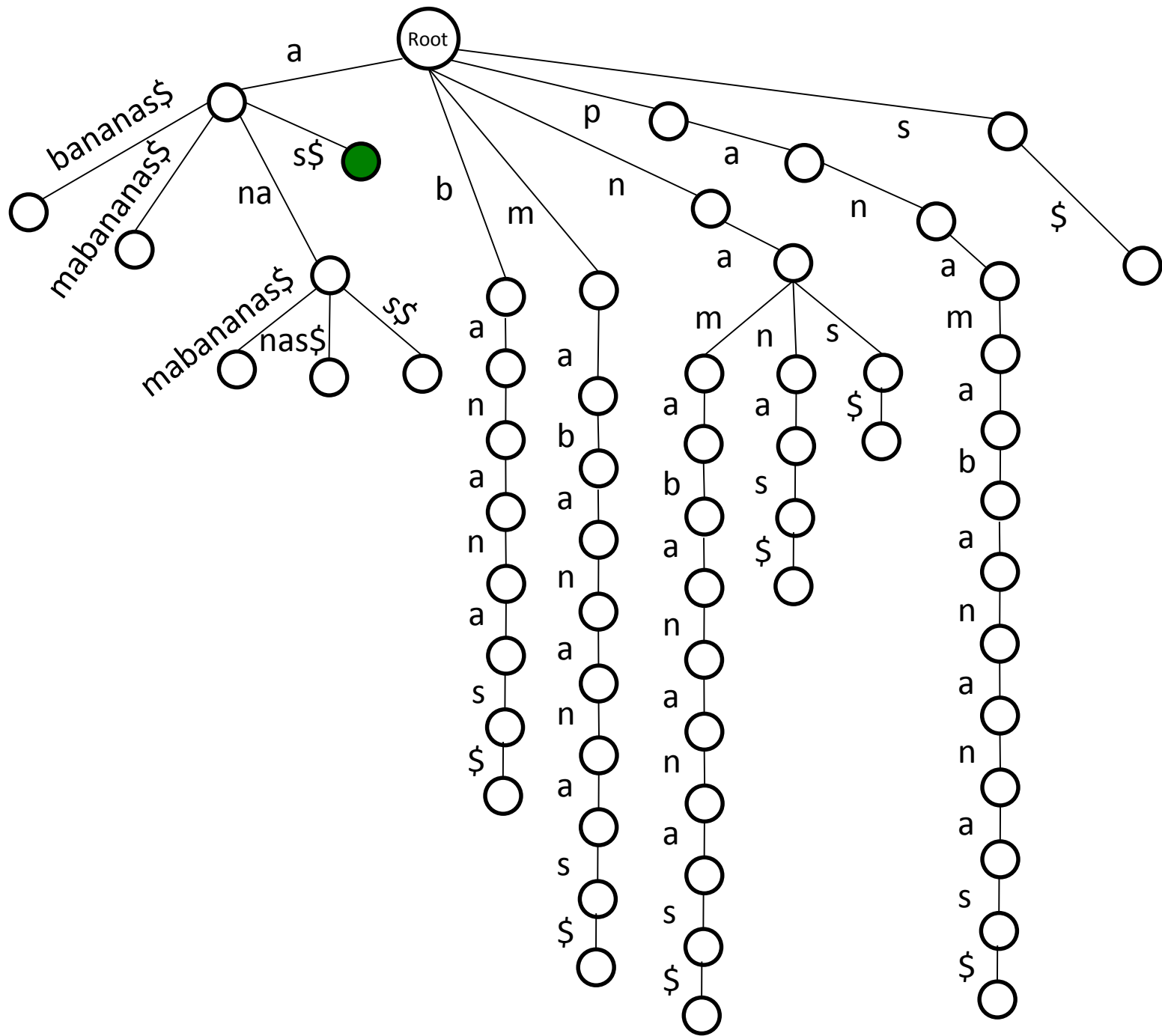


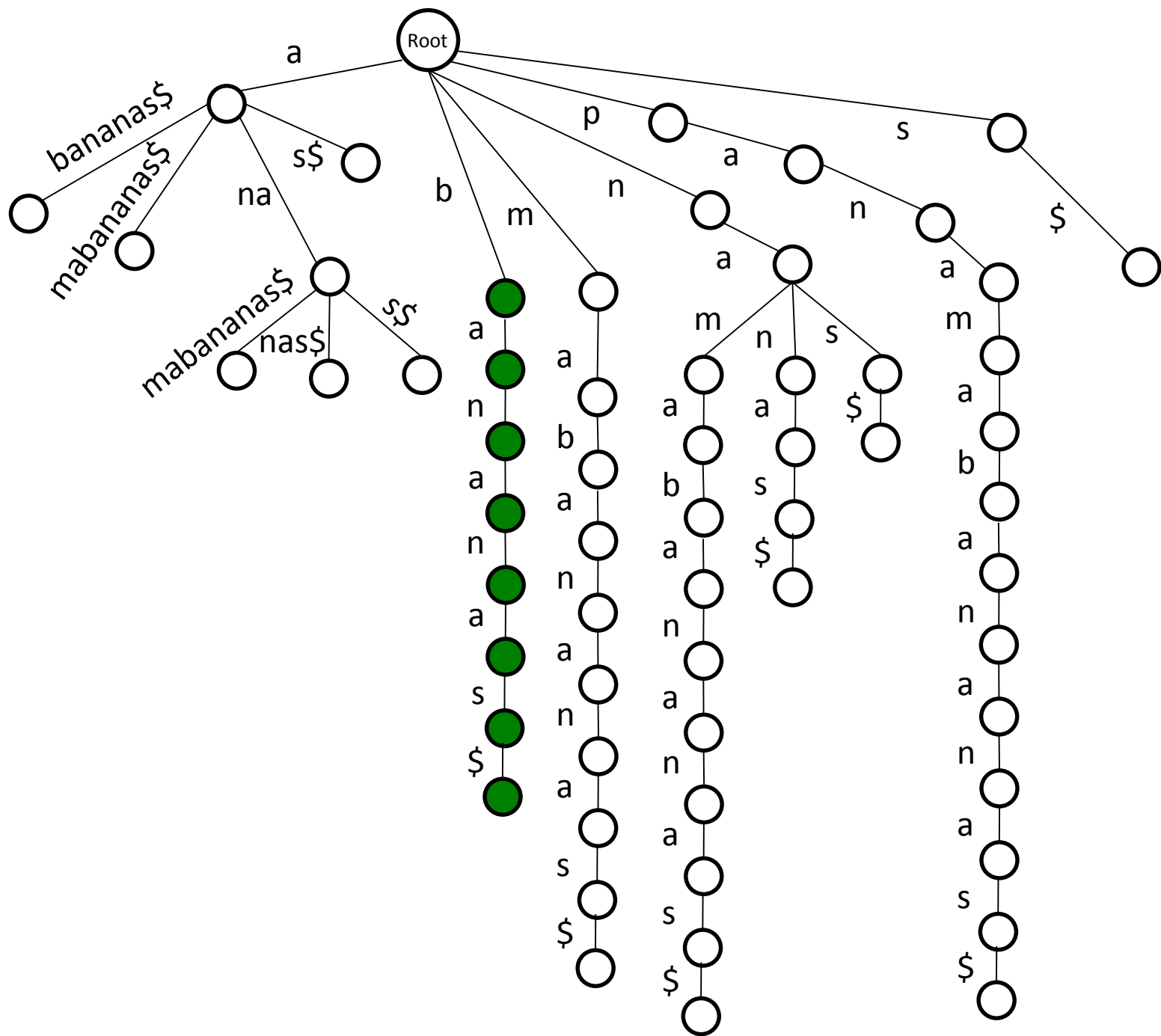


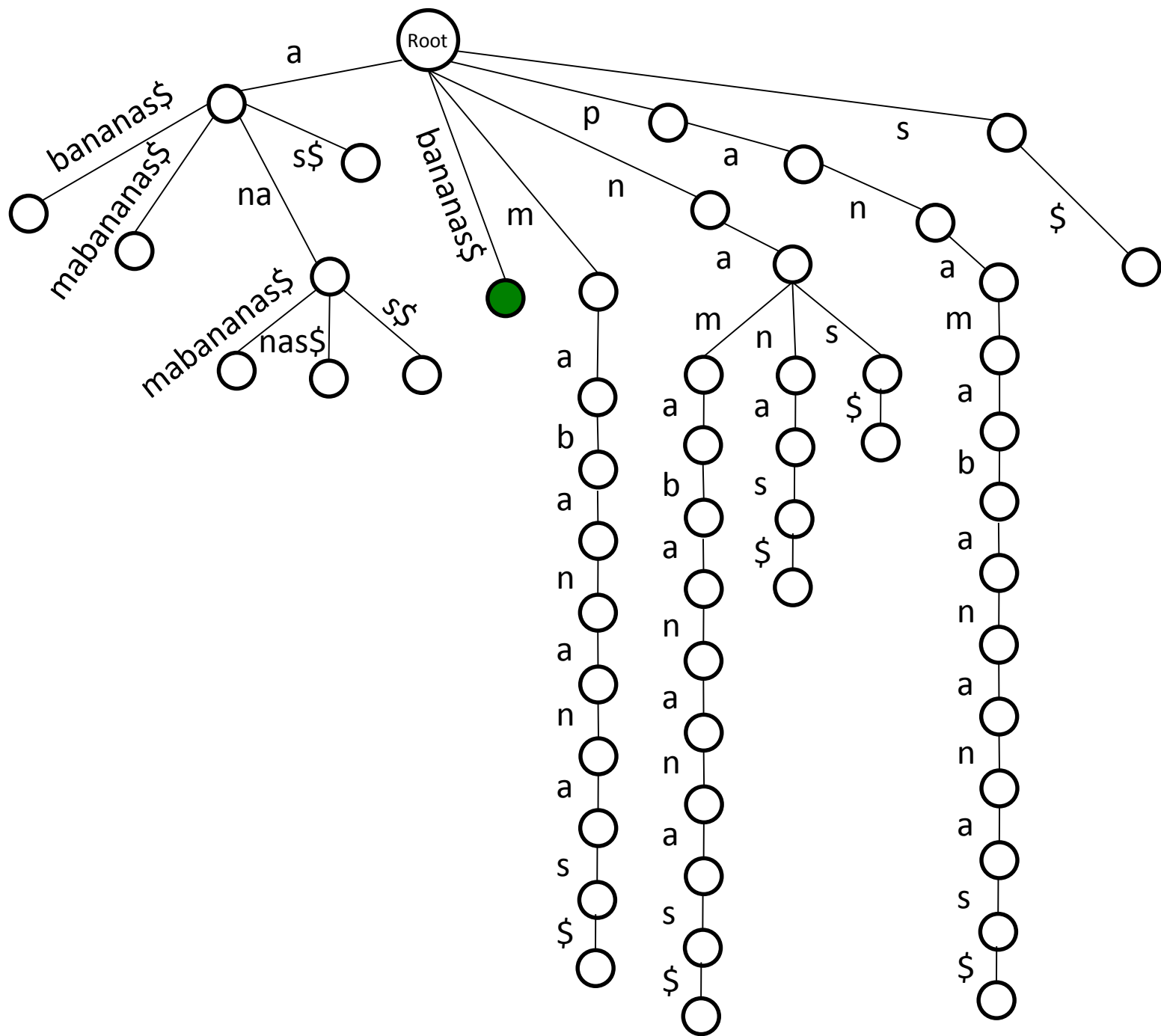


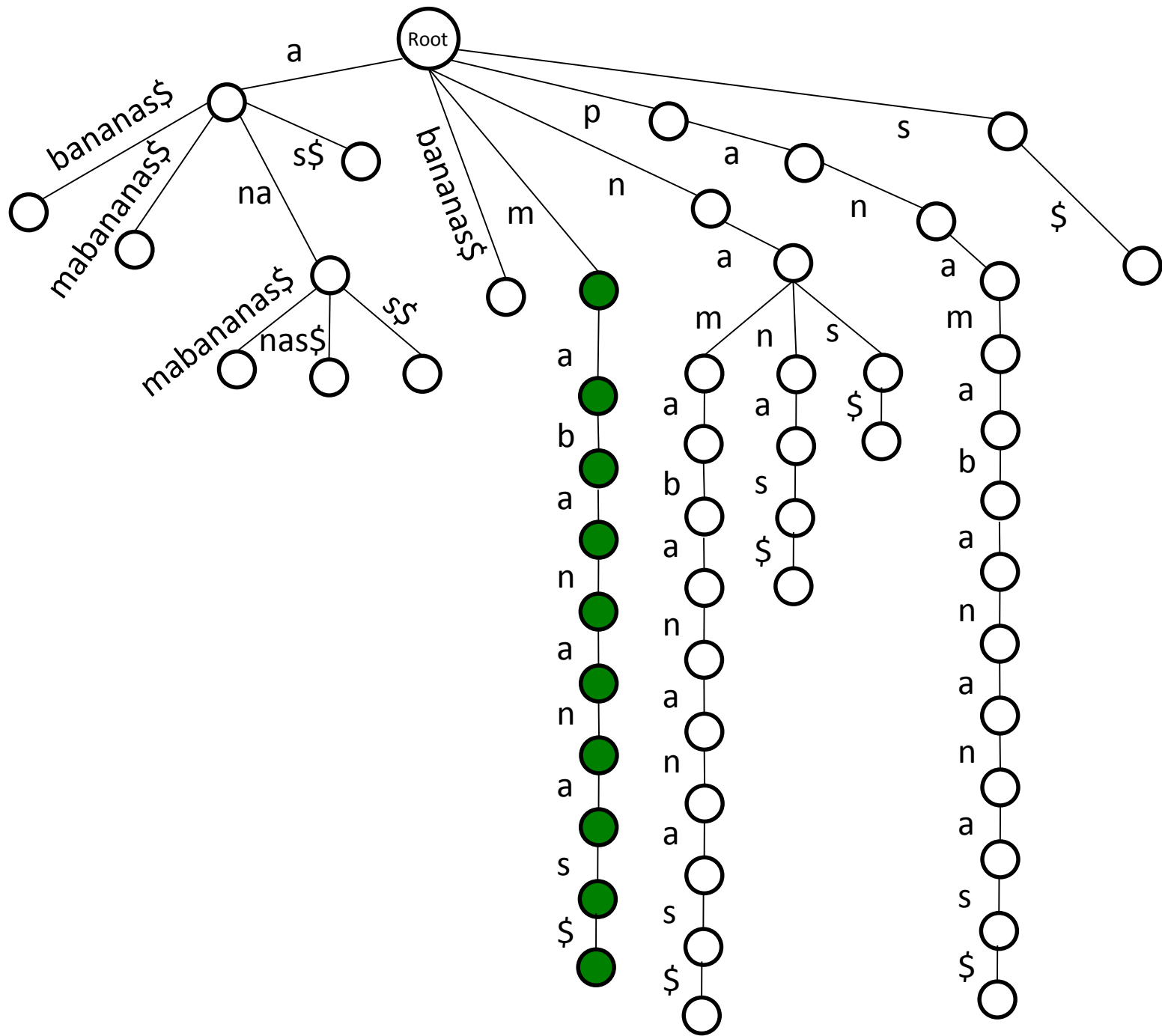


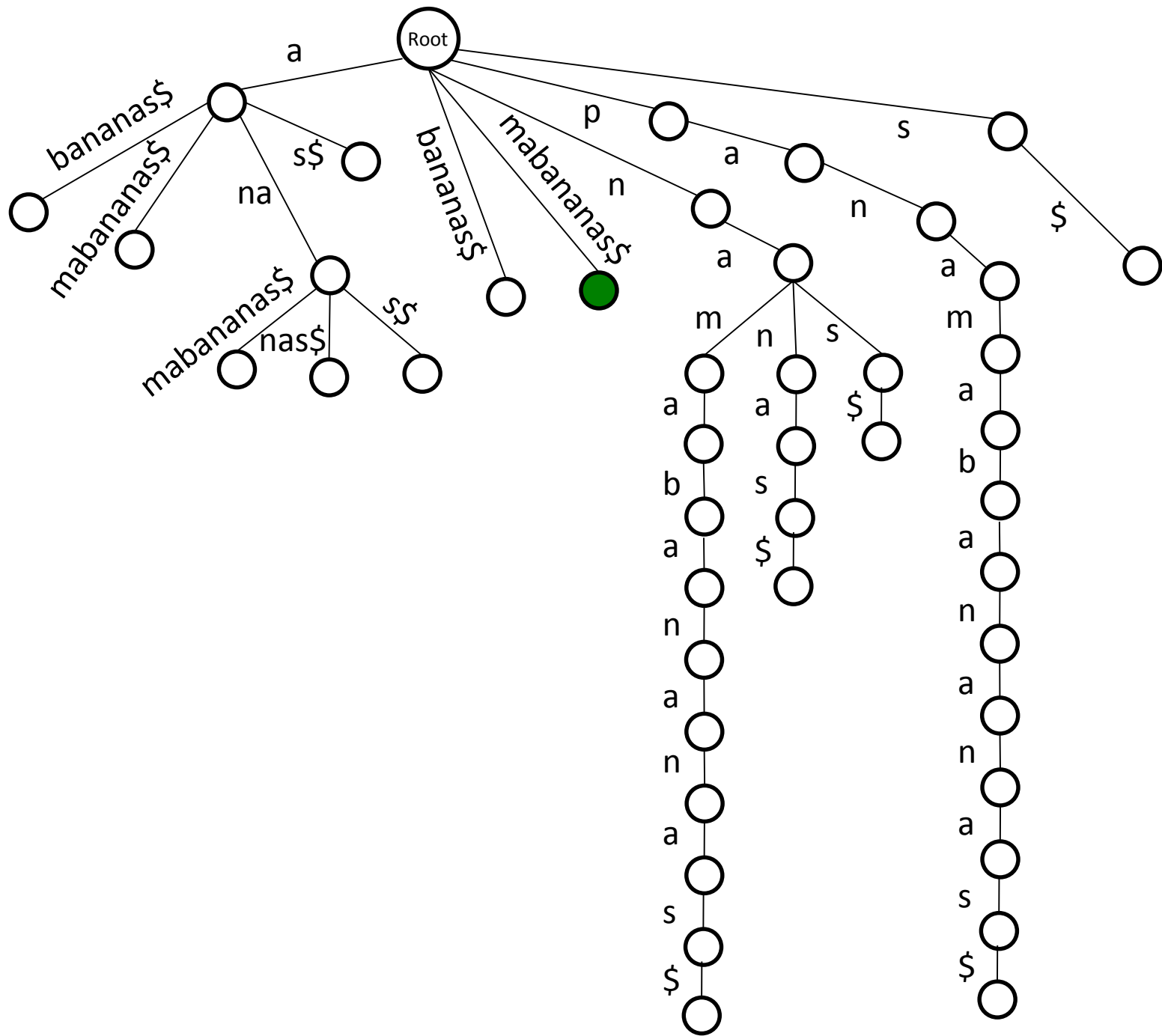


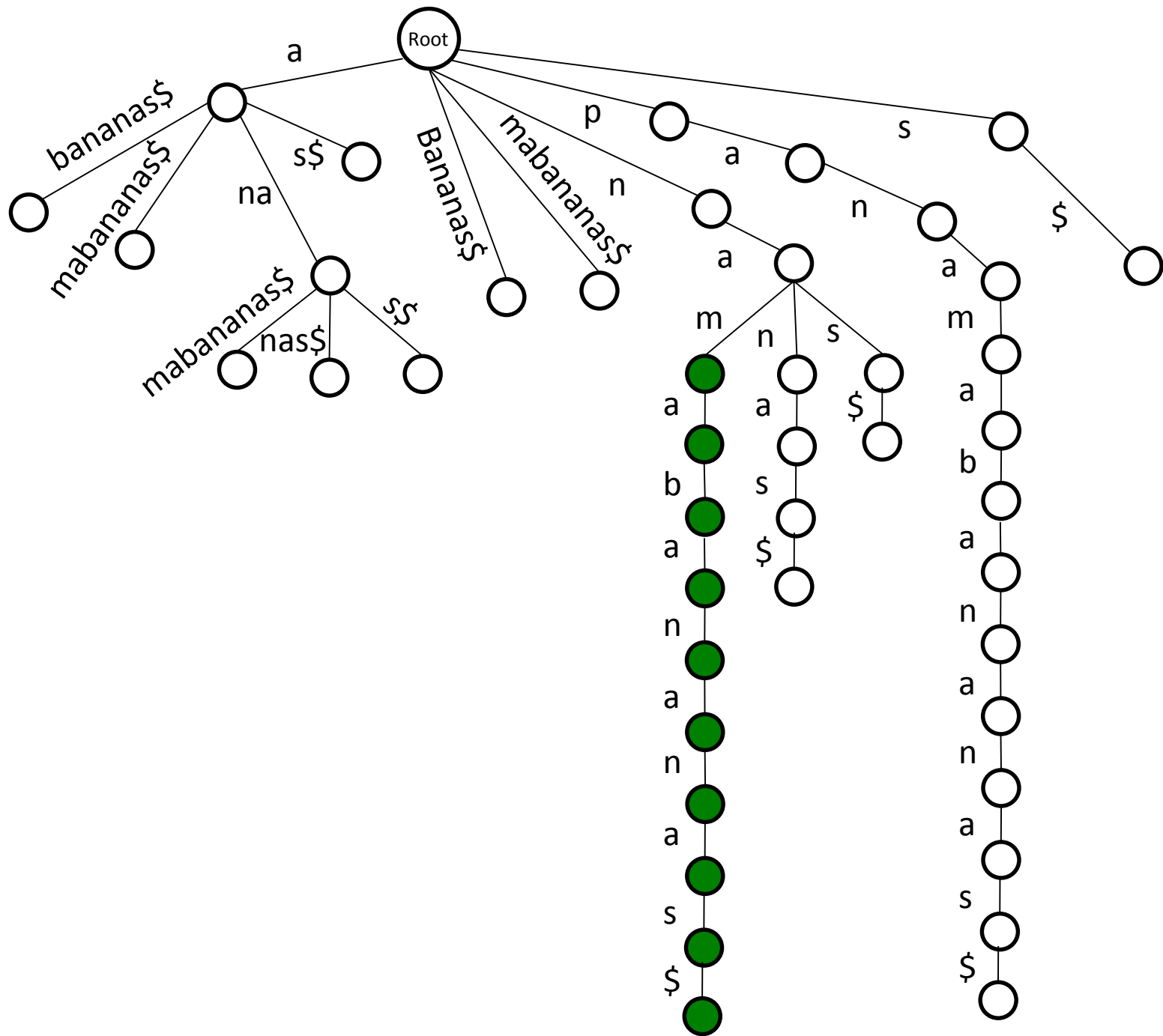


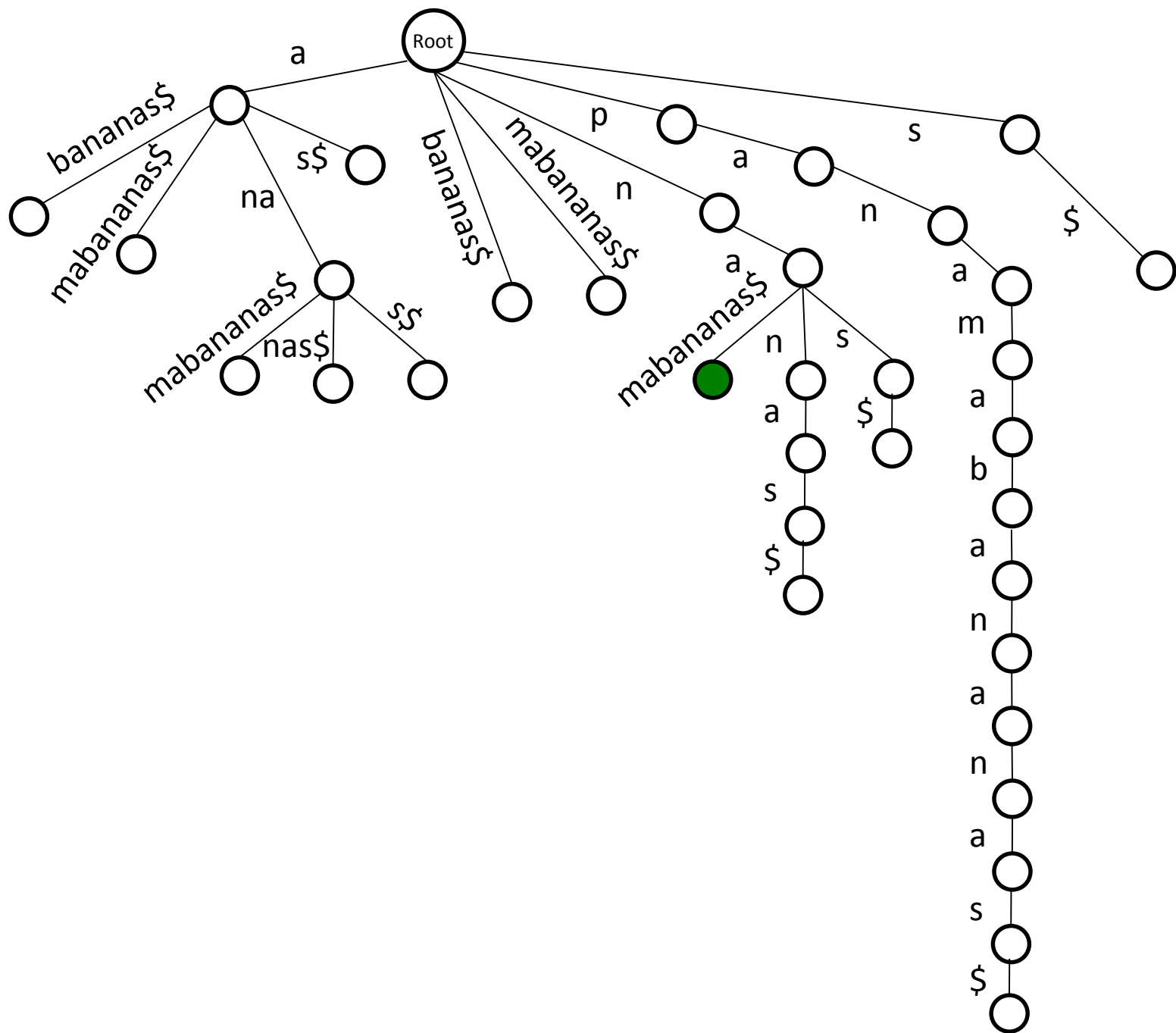


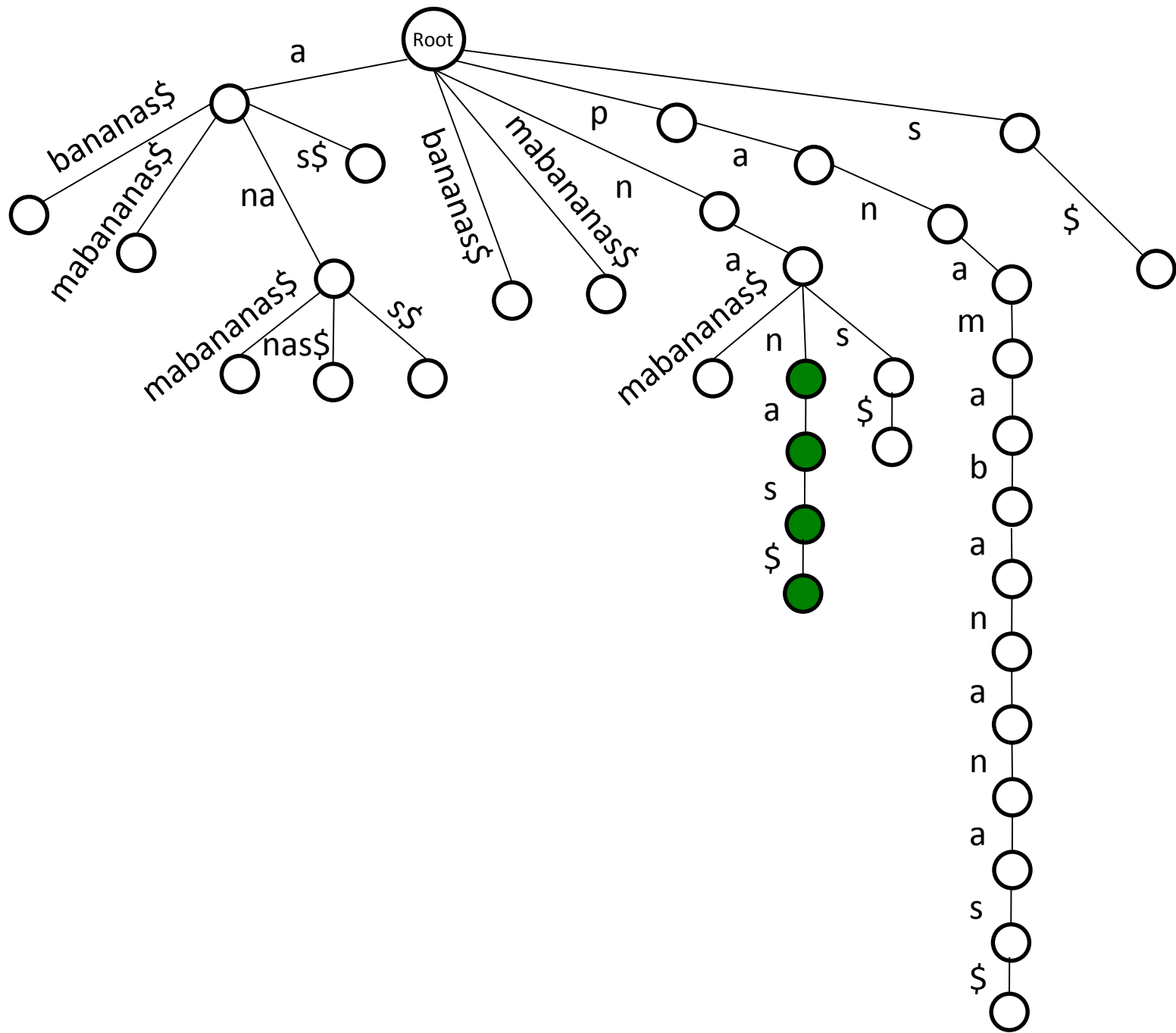


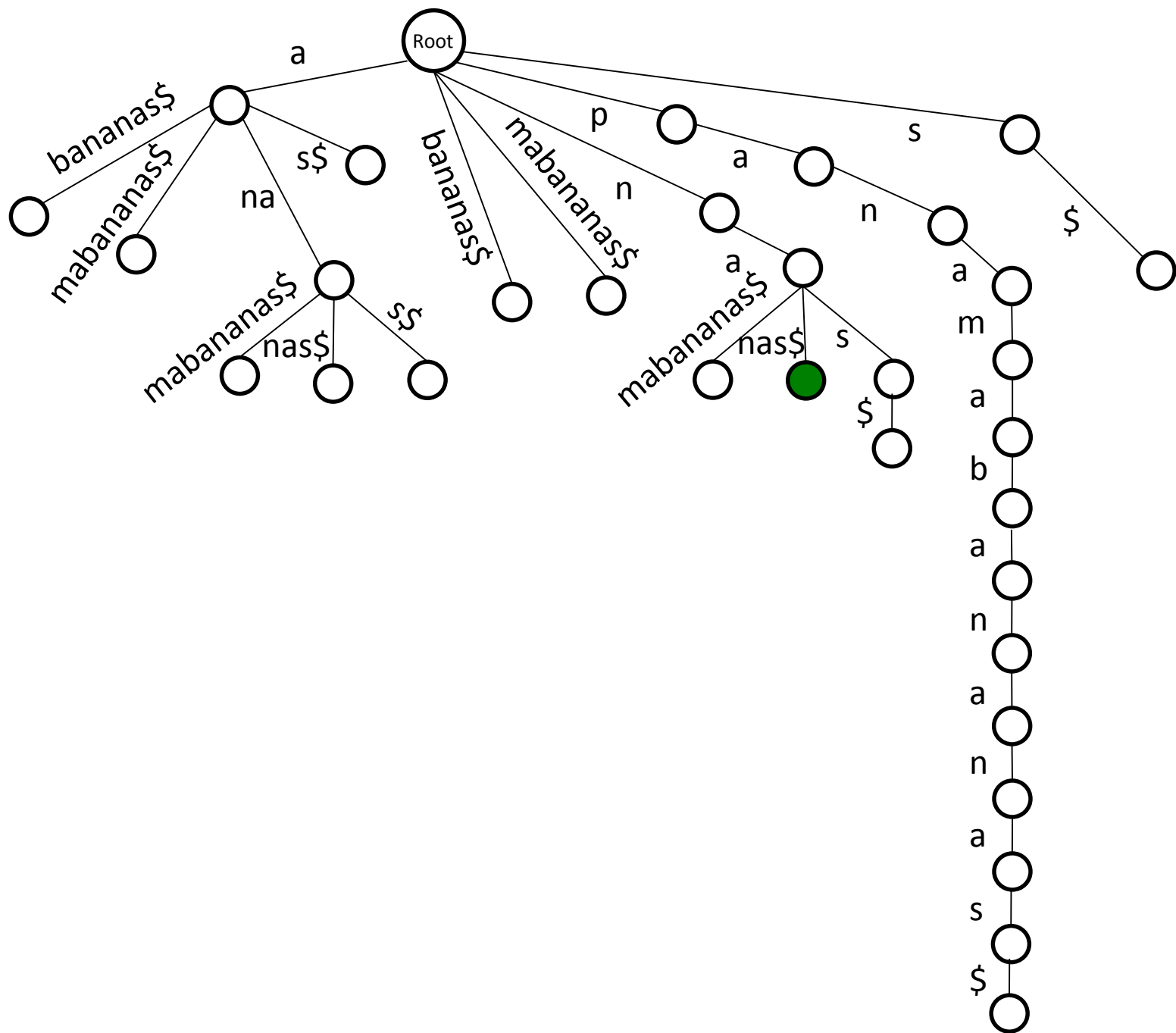


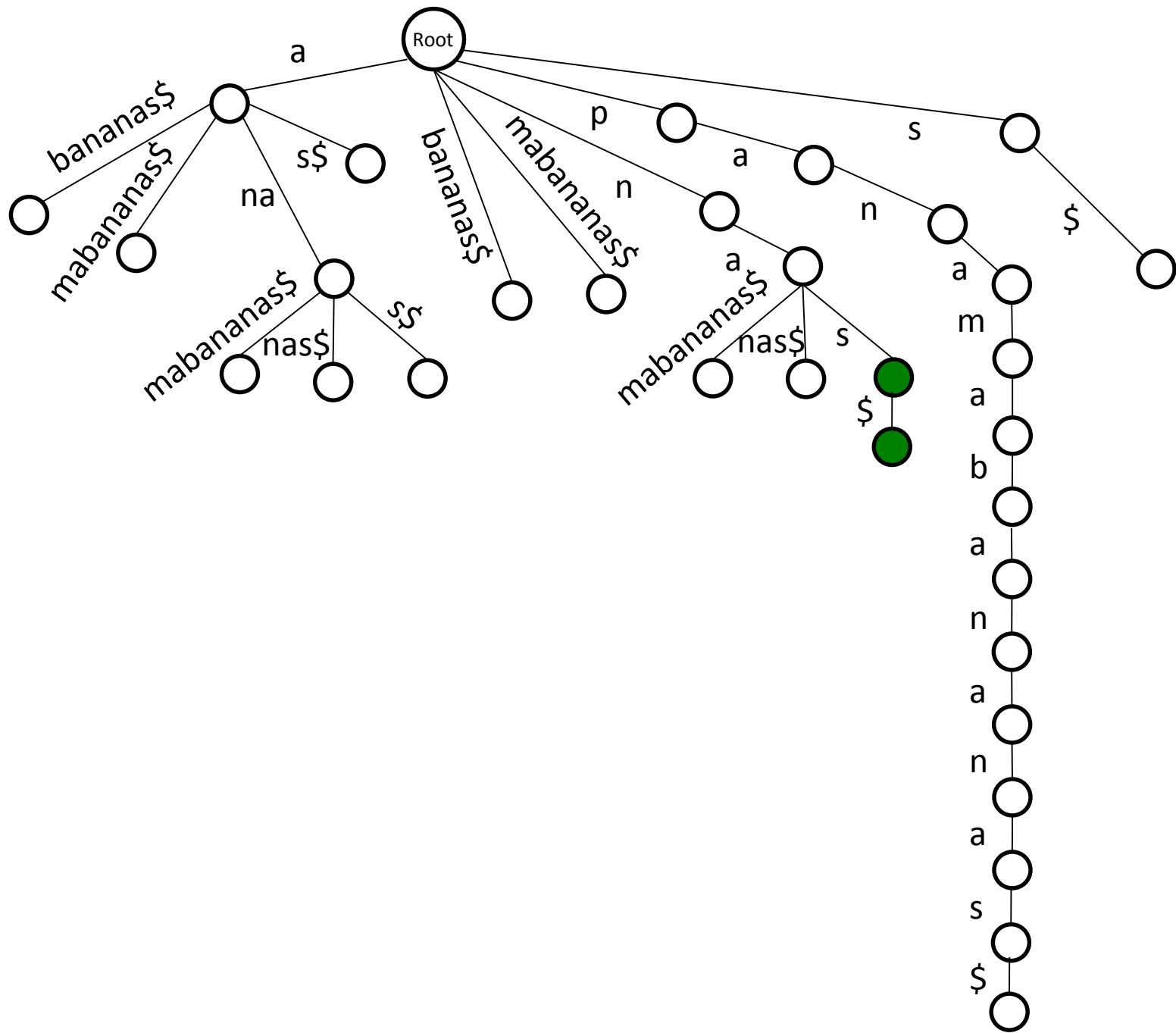


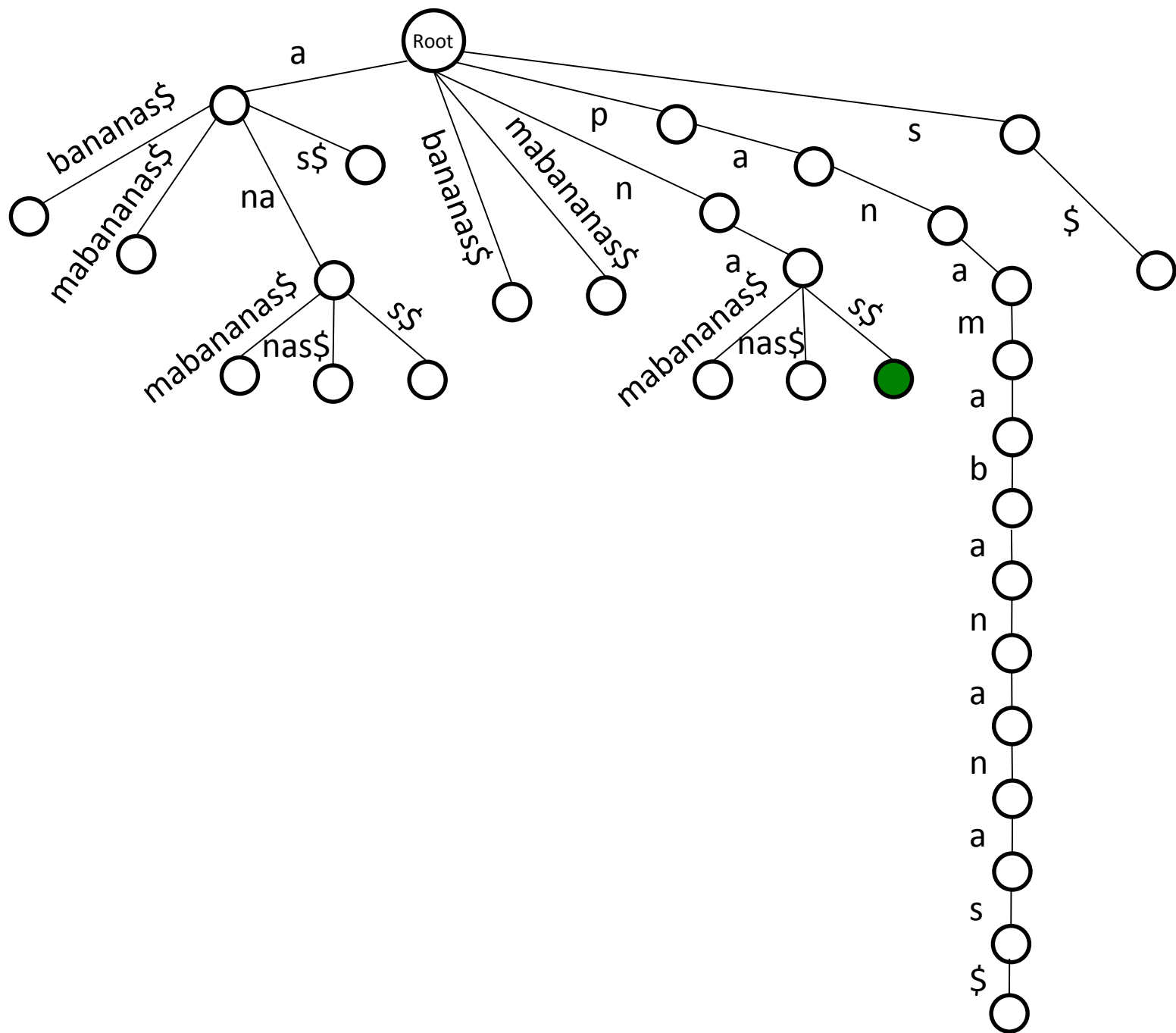


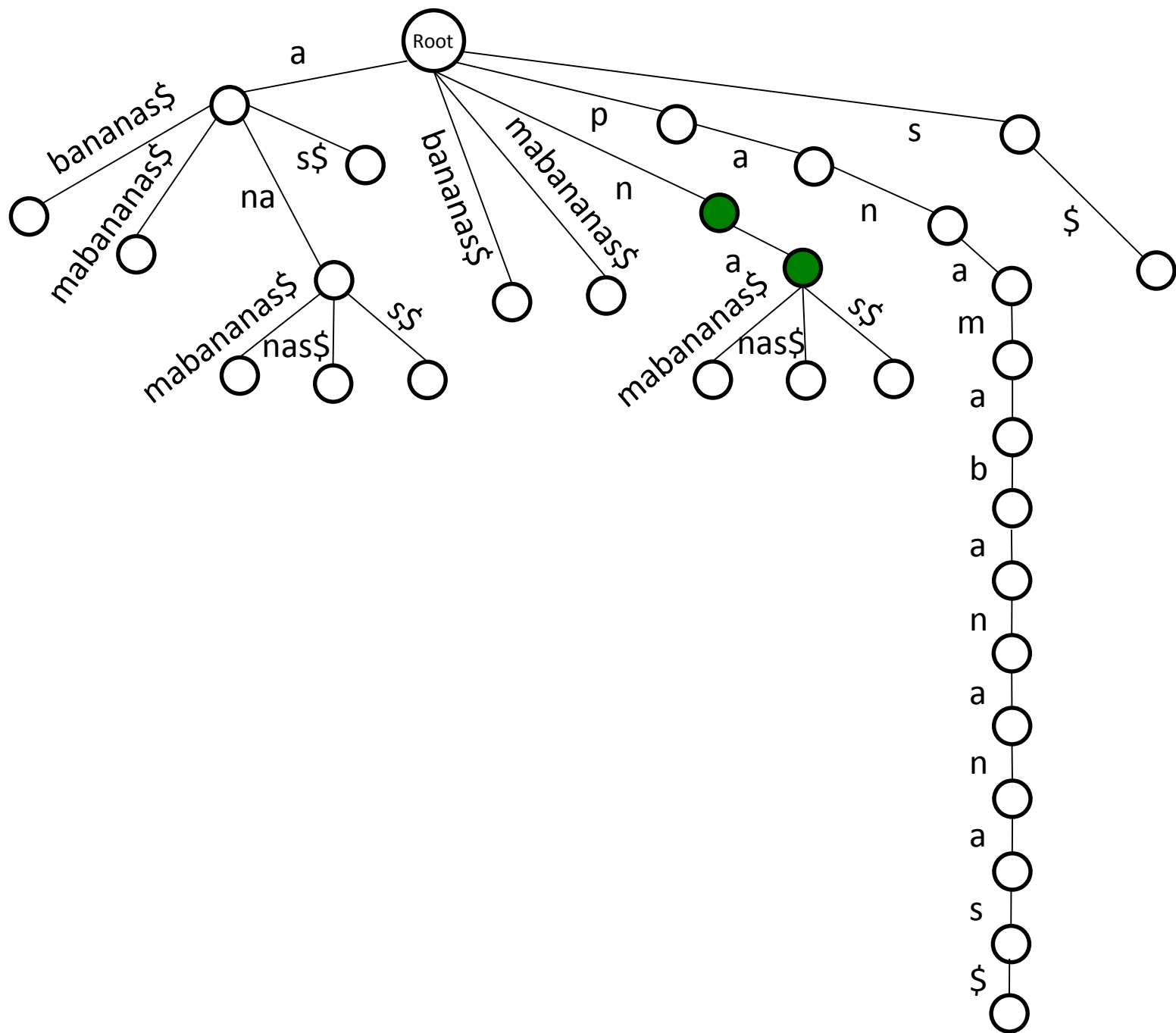


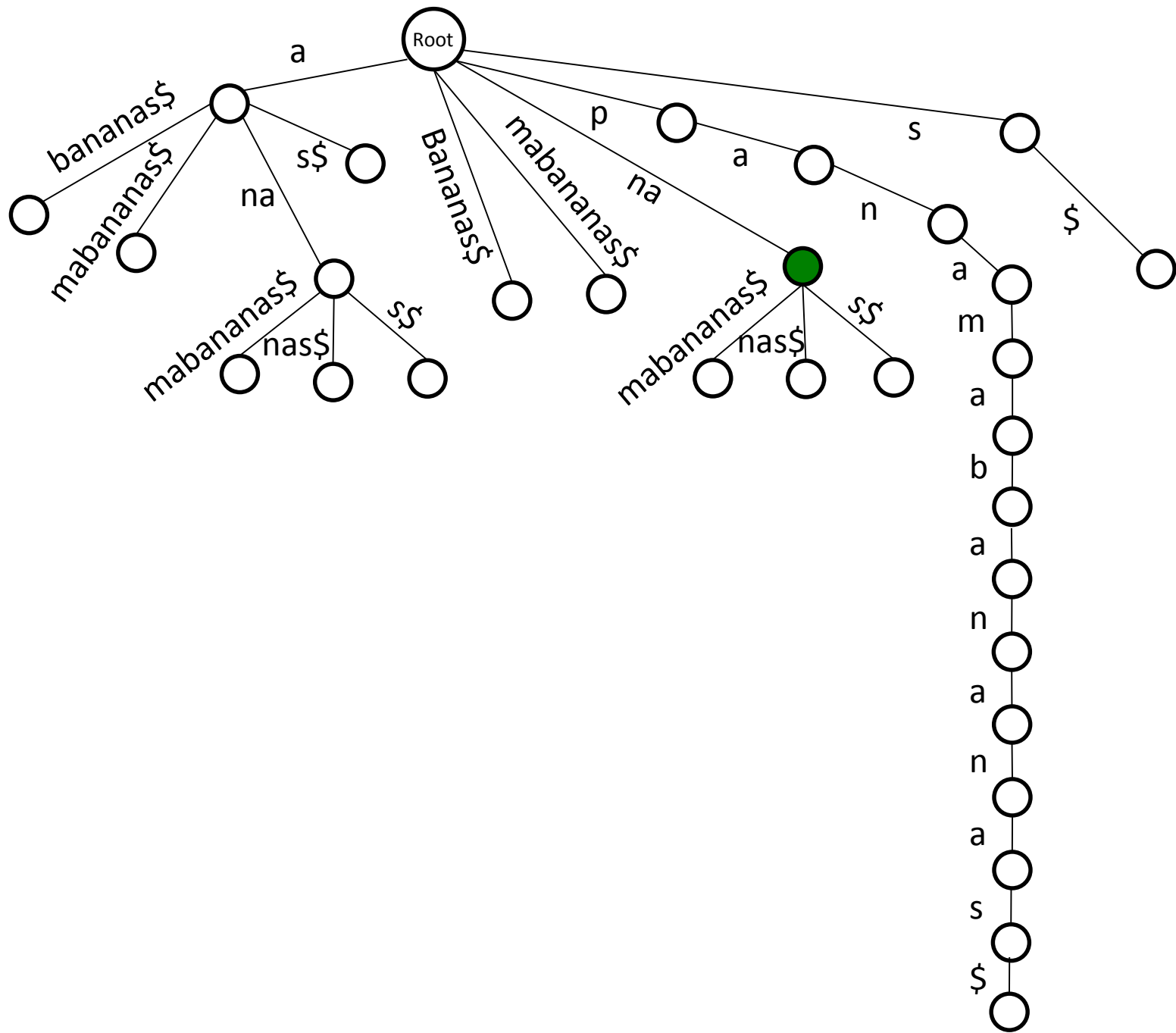


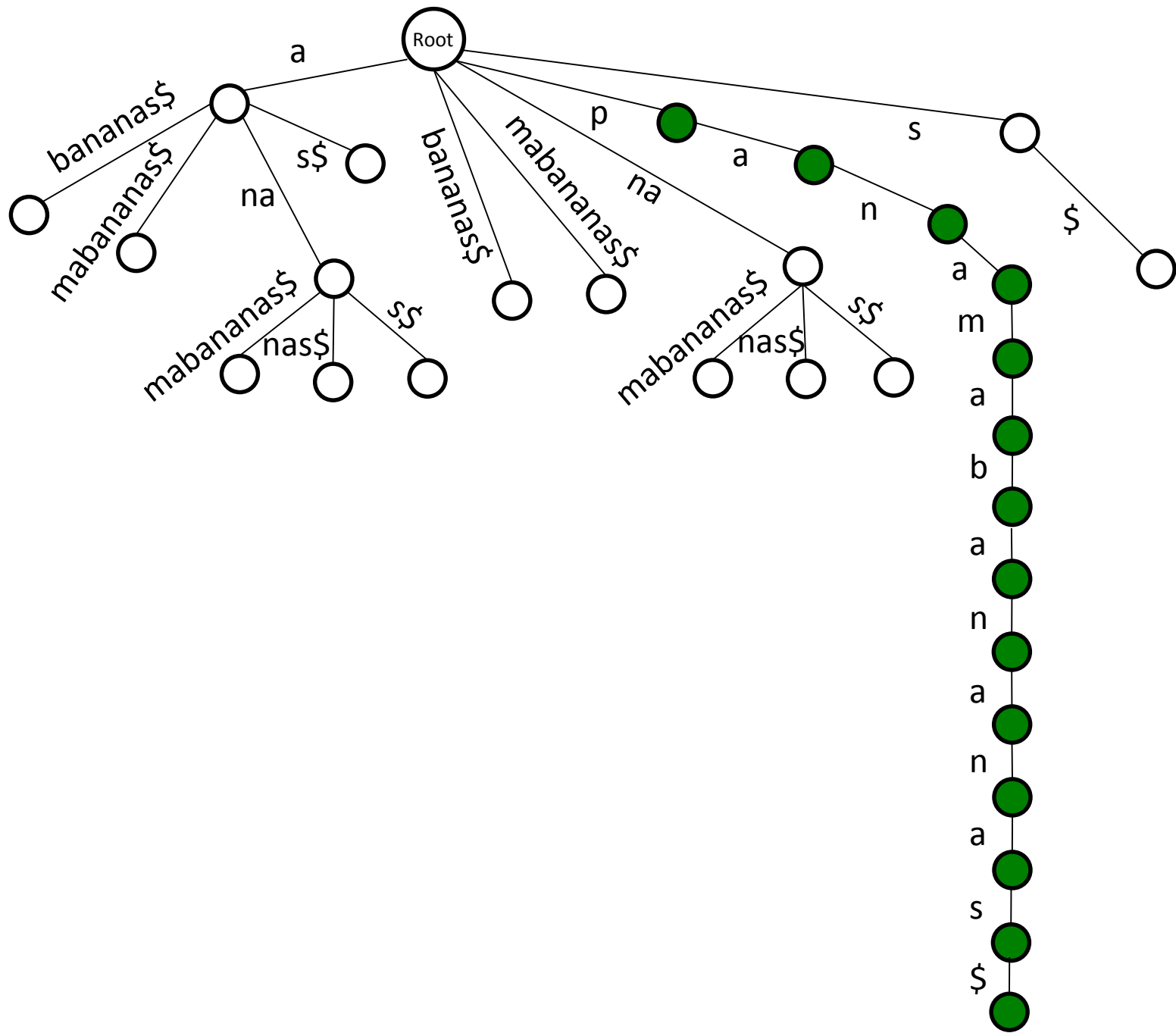


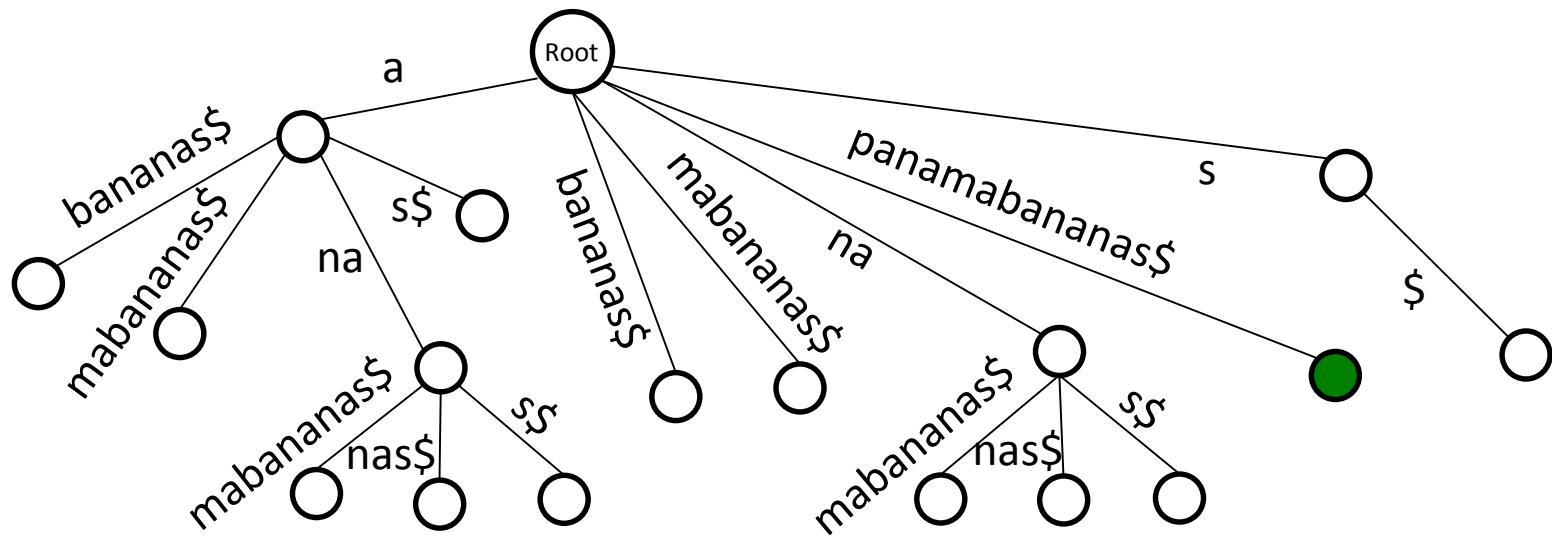


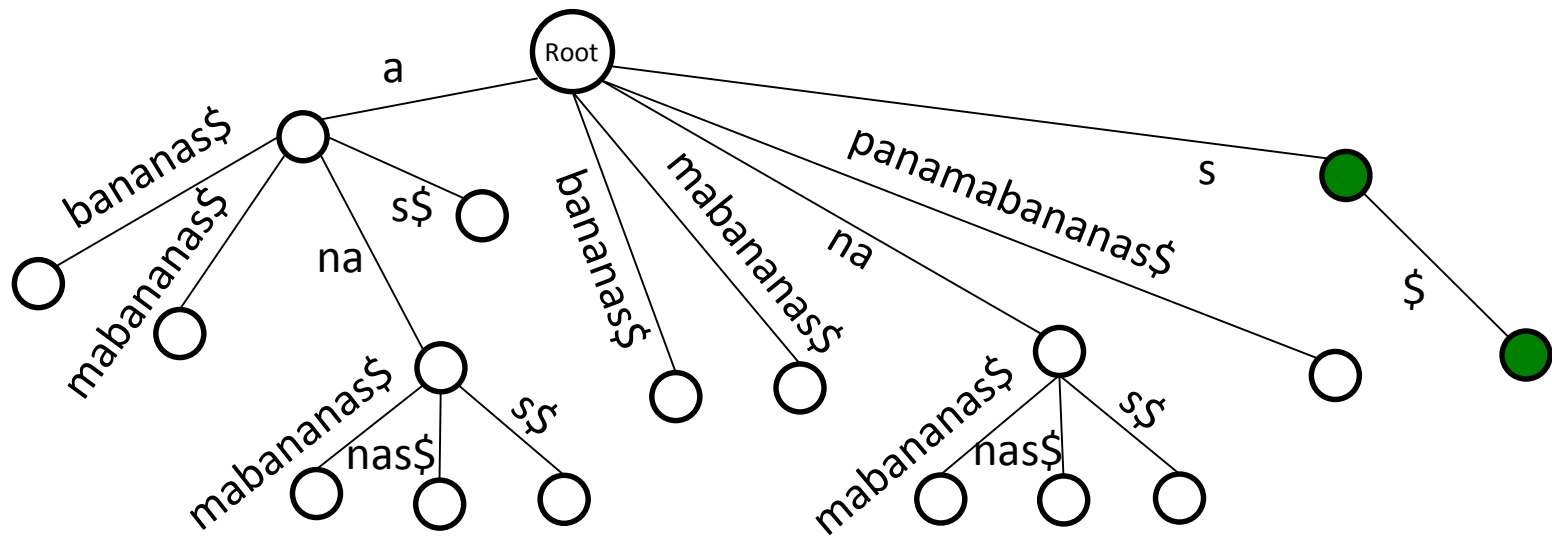


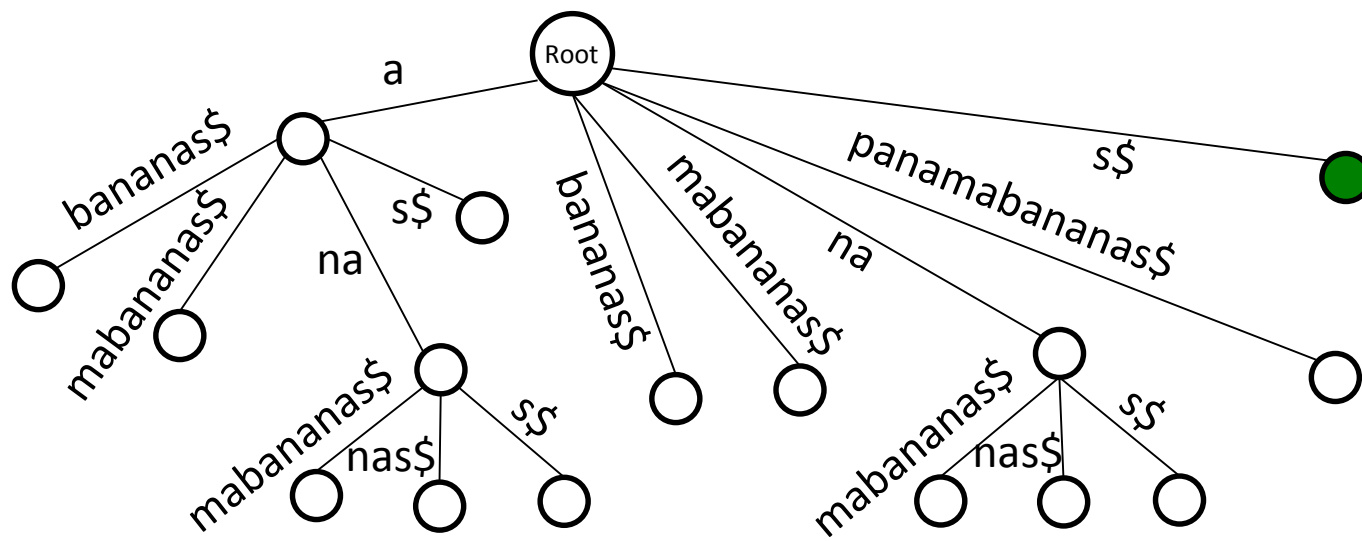




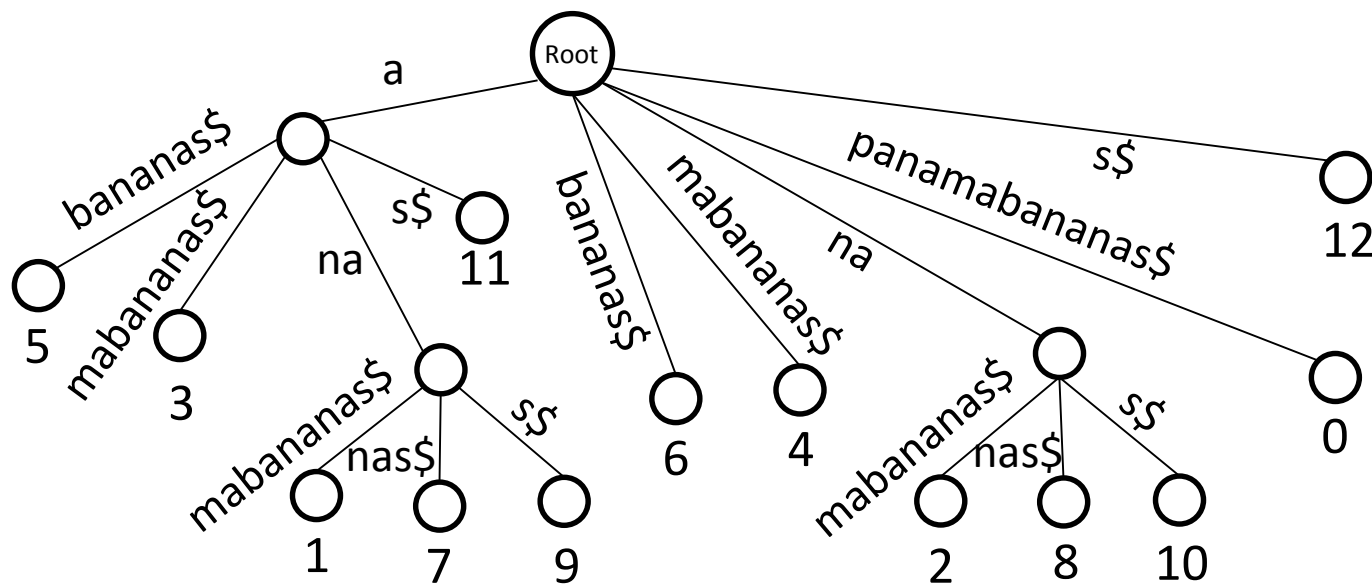






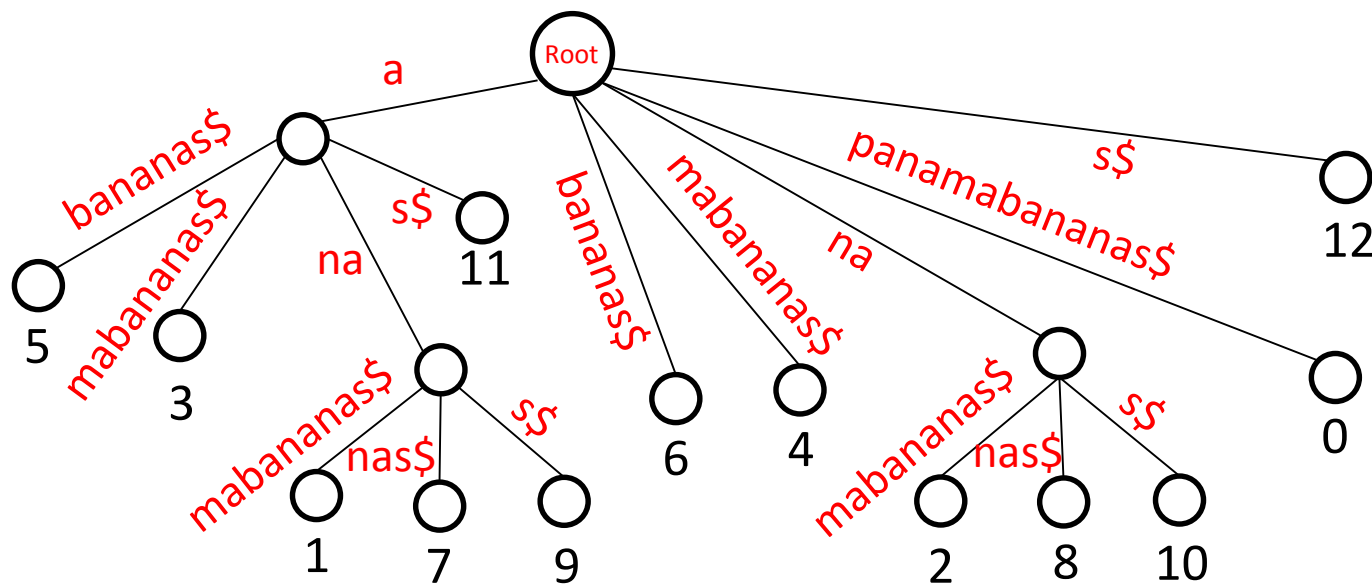


SuffixTree(*Text*)



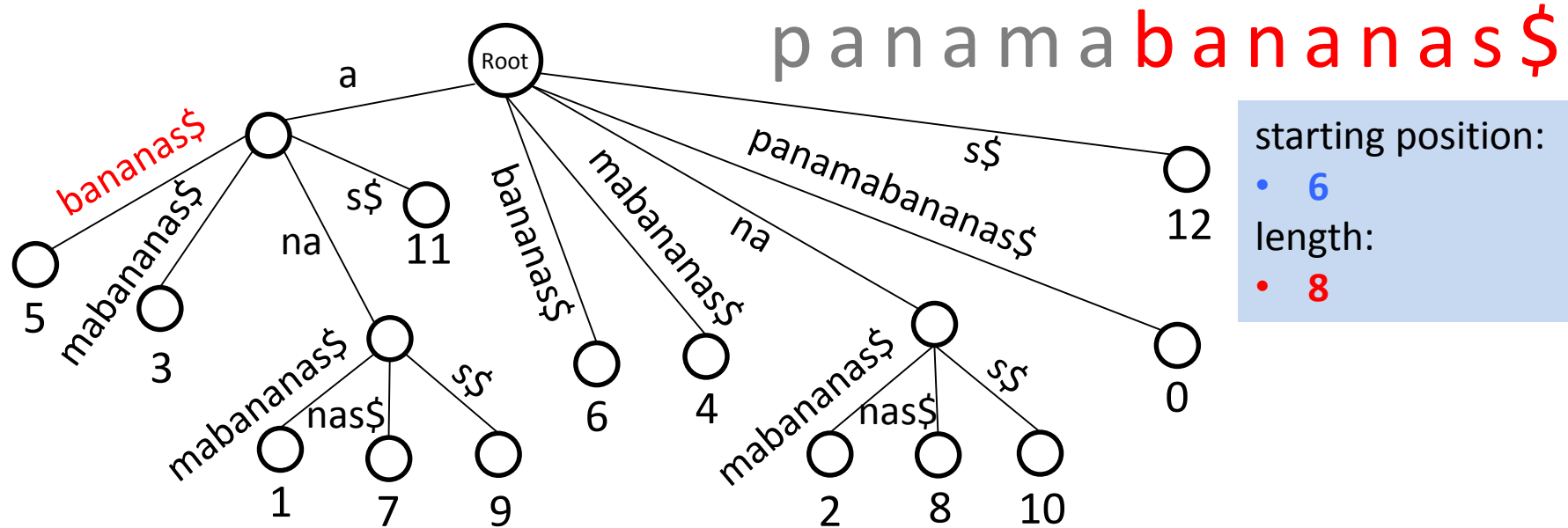
Since each suffix adds one leaf and at most one internal vertex to the suffix tree:

- $\# \text{ vertices} < 2|Text|$
- memory footprint of the suffix tree: $O(|Text|)$



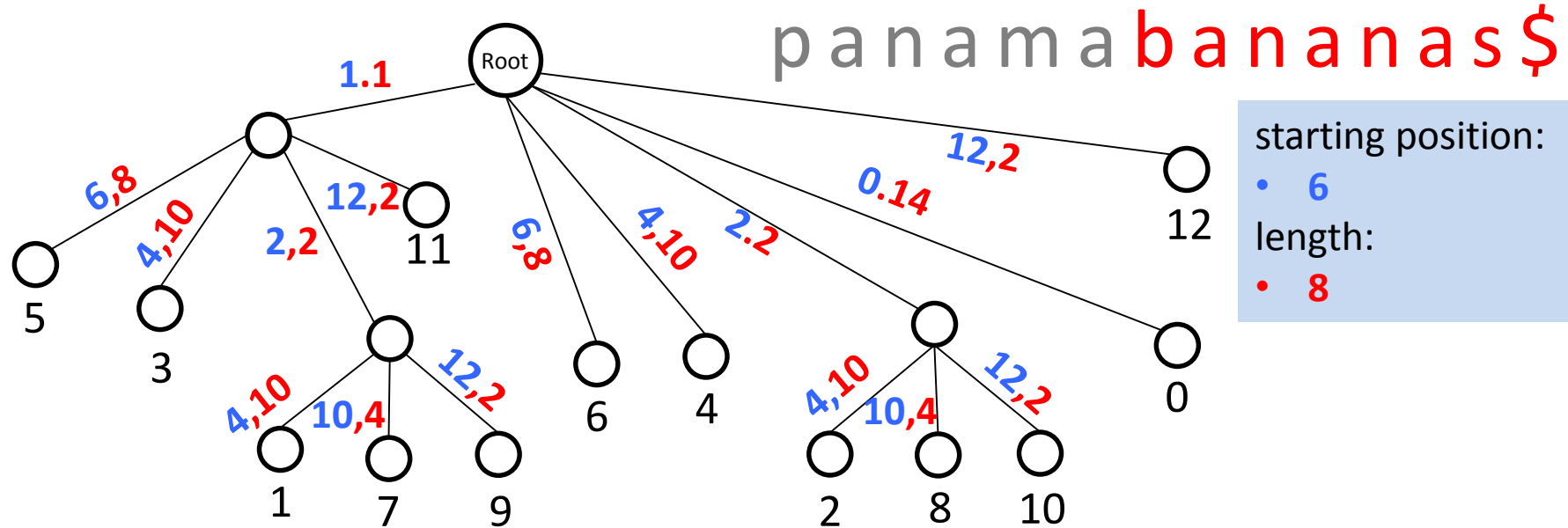
Since each suffix adds one leaf and at most one internal vertex to the suffix tree:

- $\# \text{ vertices} < 2 | \text{Text} |$
- memory footprint of the suffix tree: $O(| \text{Text} |)$
- **Cheating!!!** - how do we store all edge labels?



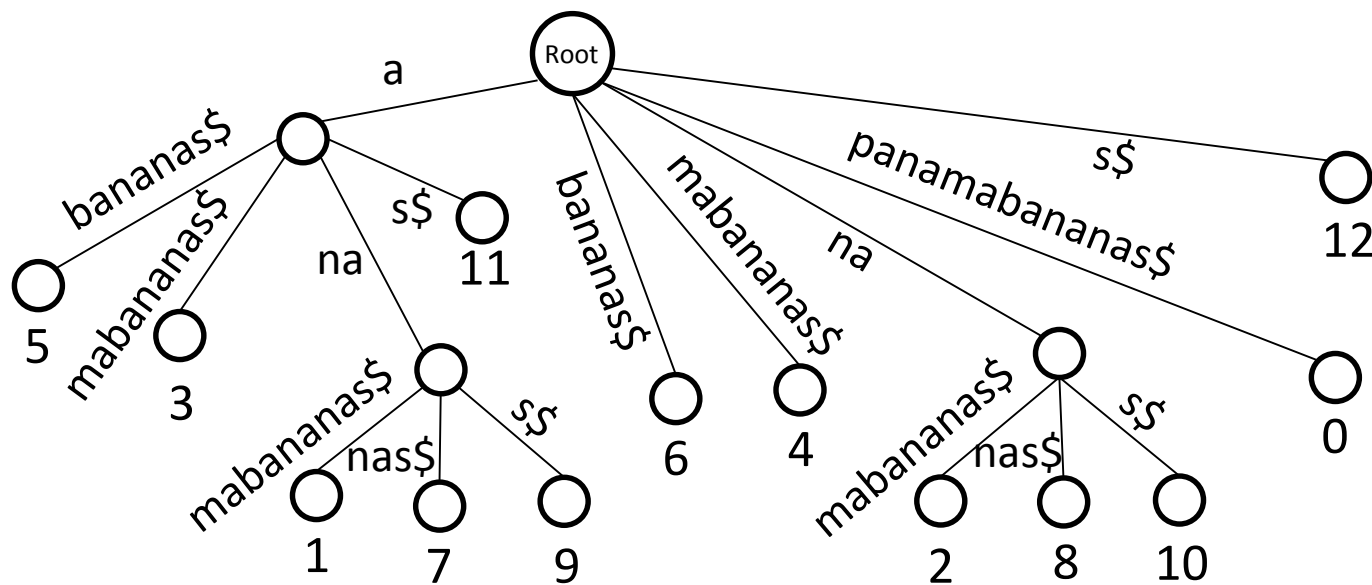
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Since each suffix adds one leaf and at most one internal vertex to the suffix tree:

- $\# \text{ vertices} < 2 | \text{Text} |$
- memory footprint of the suffix tree: $O(| \text{Text} |)$
- storing edge labels



Why did we bother to add “\$” to “panamabanananas”?

- to make sure that each suffix corresponds to a leaf

Why do we want to make sure that each suffix correspond to a leaf?

- construct suffix tree for “papa”(without adding “\$”) and compare it with the suffix tree for “papa\$”

Constructing Suffix Tree: **Naive Approach**

- **Quadratic runtime:**
 - $O(|Text|^2)$

$O(|Genome| + |Patterns|)$ to find pattern matches

Constructing Suffix Tree: **Linear-Time Algorithm**

- **Linear** runtime (for a constant-size alphabet):
 - $O(|Text|)$



Linear-time algorithm (Weiner, 1973) was simplified by Ukkonen (1995)
but it is still too complex to cover in this course

Big Secret of the Big O Notation

- Suffix trees enable fast **Exact** Multiple Pattern Matching:
 - Runtime: $O(|Text| + |Patterns|)$
 - Memory: $O(|Text|)$
- However, big-O notation hides constants!
 - suffix tree algorithms has large memory footprint
~ $20 \bullet |Text|$ for long texts like human genome
- We want to find mutations!
 - it is unclear how to develop fast **Approximate** Multiple Pattern Matching using suffix trees