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ON THE STABILITY OF AN ENEMY – AMMENSAL SPECIES PAIR WITH RESOURCES LIMITED FOR ONE SPECIES AND UNLIMITED FOR THE OTHER

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Abstract

The Ammensal species (S_1), in spite of its natural resources gets adversely effected due to interaction with the enemy species (S_2). In this paper two mathematical models of Ammensalism between two species are investigated. The two cases considered are 1) S_1 with limited resources and S_2 with unlimited resources; 2) S_1 with unlimited resources and S_2 with limited resources. These models are characterized by a pair of first order non-linear coupled differential equations. In each of the cases there exist only two equilibrium points and the criteria for their stability are discussed. The results are compared with author's earlier work with limited resources.

Introduction

Ecology is a branch of science, which studies the interactions among living beings in the same habitat along with their living style. Research in theoretical ecology was initiated by Lotka [11] and by Volterra [16]. Many mathematicians and ecologists with their zeal and quest followed them contributing their might to the growth of this area of knowledge as reported in the treatises of Meyer [12], Kushing [8], Paul colinvaux [13], Kapur [6,7] etc. The ecological interactions can be broadly classified as Prey – predation, competition, Commensalism, Ammensalism, and Neutralism and so on. N.C. srinivas [16] studied competitive eco-systems of two and three species with limited and unlimited resources. Later, Lakshminarayan [9], Lakshminarayan and Pattabhi Ramacharyulu [10] studied Prey-predator ecological models with a partial cover for the prey and alternate food for the predator. Recently, some studies on stability analysis of competitive species were carried out by Archana Reddy[2,3], Pattabhi Ramacharyulu and Gandhi[2] and by Bhaskara Rama Sharma[4,5]., and Pattabhi Ramacharyulu[4].,while Ravindra Reddy[15] investigated mutualism between two species. Phani Kumar and Pattabhi Ramacharyulu [14] obtained some results on the stability of a host- a flourishing commensal species pair with limited resources. Acharyulu and Pattabhi Ramacharyulu[1] investigated some results on stability of an enemy and Ammensal species pair with limited resources.

The present investigation is related to an analytical study of Ammensalism between two species and this is a continuation of the work cited in [1]. Ammensalism is an ecological relationship between two species where one species (S_1) adversely effects by other species S_2 without being effected by it: S_1 may be referred as the Ammensal species while S_2 the enemy. The following are Some examples of Ammensalism: 1) when penicillum (bread mold), secretes penicillin and kills bacteria. The penicillum does not get any benefit from killing the bacteria.2) Algal blooms can lead to the death of many species of fish, however the algae do not benefit from the deaths of these individuals.

.The Ammensal species (S_1), in spite of its natural resources, declines in its strength from the enemy species (S_2) which is not effected by S_1. .These models are characterized by a coupled pair of first order non-linear differential equations. The two equilibrium points are identified. There is no co-existence state. The criteria for the the stability are established in each case. it is noticed that the stability is conditional in the following situations. I) the Ammensal species (S_1) with limited resources while the enemy species (S_2) has unlimited resources. i) the death rates are greater than the respective birth rates of both the species in the fully washed out state ii) the death rate of enemy species is greater than its birth rate when the ammensal survives and the enemy species is washed out state .II) the Ammensal species (S_1) with unlimited resources while the enemy species (S_2) has limited resources i) the death rates are greater than the respective birth rates of both the species in the fully washed out state. ii) The enemy survives and the Ammensal species is washed out state. The linearised perturbed equations are solved and the trajectories are illustrated. The results are compared with the results obtained earlier by the present authors [1] in the case where the resources for both the species are limited.

Notation adopted:

N_1, N_2 : The populations of the Ammensal (S_1) and enemy (S_2) species respectively at time t

a_1, a_2 : The natural growth rates of S1 and S_2

a_{11}, a_{22} : The self inhibition coefficients of N_1 and N_2

a_{12} : The Ammensal coefficient.

k_{11} (= a_1/ a_{11}); k_{22} (= a_2 / a_{22}): the carrying of capacities of N1 and N_2

t* : The dominance-reversal time of one species over the other

$\bar{N}_1, \bar{N}_2$: The equilibrium values of N_1 and N_2 (given by $\dot{N}_1 = 0$, $\dot{N}_2 = 0$)

U_1 (t), U_2 (t): Small perturbations in N_1 and N_2 over the equilibrium values

Further both the variables N_1 and N_2 are non-negative and the model parameters a_1, a_2, a_{11}, a_{22} and a_{12} are assumed to be non-negative constants.

I)The Ammensal species (S_1) with limited resources and the enemy species(S_2) with unlimited resources

This is the case with $k_1 < \infty$ and $k_2 \to \infty$ i.e., when $a_{11} \neq 0$ and a22 = 0

A) Basic Equation for the growth rate of the Ammensal species (S_1)

$$\frac{dN_1}{dt} = a_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2 \qquad (A.1)$$

Basic Equation for the growth rate of enemy species (S_2)

$$\frac{dN_2}{dt} = a_2 N_2 \qquad (A.2)$$

The system has only two equilibrium states defined by $\frac{dN_1}{dt}=0$, $\frac{dN_2}{dt}=0$. (A.3)

The equilibrium points are obtained as

$E_1^{(I)}$: $\bar{N}_1 = 0$; $\bar{N}_2 = 0$ [Fully washed out state] (A.4)

$E_2^{(I)}$: $\bar{N}_1 = \frac{a_1}{a_{11}}$; $\bar{N}_2 = 0$ [The Ammensal survives and enemy is washed out.] (A.5)

B) The Stability of the Equilibrium State $E_1^{(I)}$.

To this end, we consider slight deviations U_1 (t) and U1 (t) over the steady state ($\bar{N}_1, \bar{N}_2$)

$N_1 = \bar{N}_1 + U_1$ (t), $N_2 = \bar{N}_2 + U_2$ (t) (B.1)

where U_1 (t) and U_2 (t) are so small that the terms other than their first terms can be neglected. Substituting in (A.1) and (A.2) and neglecting products and higher powers of U_1 and U_2 we get

$$\left.\begin{aligned}\frac{dU_1}{dt} &= a_1 U_1\\ \frac{dU_2}{dt} &= a_2 U_2\end{aligned}\right\} \quad \text{(B.2)}$$

the characteristic equation for which is

$$(\lambda - a_1)(\lambda - a_2) = 0, \quad \text{(B.3)}$$

whose roots a_1, a_2 are both positive. Hence the steady state is **unstable**.

For solving (B.2), we get $U_1 = U_{10}\, e^{a_1 t}$; $U_2 = U_{20}\, e^{a_2 t}$ (B.4)

where U_{10}, U_{20} are initial values of U_1, U_2 respectively.

The solution curves are illustrated in Fig. (1) to (4) and the conclusions are presented in **TABLE-1.**

TABLE- 1

	$a_1 > a_2$	$a_1 < a_2$
$U_{10} > U_{20}$	The Ammensal (N_1) dominates over the enemy (N_2) in natural growth rate as well as in its initial population strength.-Fig (1).	The Ammensal (N_1) dominates over the enemy (N_2) in natural growth rate but it's initial strength is less than that of an enemy, and the enemy out numbers the Ammensal till the time-instant $t^* = \frac{1}{a_2 - a_1}\log\left(\frac{U_{10}}{U_{20}}\right)$ after that the dominance is reversed .-Fig (2).
$U_{10} < U_{20}$	The enemy(N_2) dominates over the Ammensal (N_1) in natural growth rate but it's initial strength is less than that of Ammensal and Ammensal out numbers the enemy till the time- instant $t^* = \frac{1}{a_2 - a_1}\log\left(\frac{U_{10}}{U_{20}}\right)$ after that the dominance is reversed.- Fig (3).	The enemy (N_2) dominates over the Ammensal (N_1) all throughout . - Fig (4).

Trajectories of Perturbed Species:

The trajectories (solution curves of B.2) in the $U_1 - U_2$ plane are given by

$$\left(\frac{U_1}{U_{10}}\right)^{a_2} = \left(\frac{U_2}{U_{20}}\right)^{a_1} \quad \text{and are shown in Fig (5).} \qquad \text{(B. 5)}$$

3.2 Stability of the Equilibrium State $E_2^{(1)}$.

The corresponding linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= -a_1 U_1 - \frac{a_1 a_{12}}{a_{11}} U_2 , \\ \frac{dU_2}{dt} &= a_2 U_2 \end{aligned}\right\} \qquad \text{(B. 6)}$$

The characteristic equation for this system is

$$(\lambda + a_1)(\lambda - a_2) = 0 \qquad \text{(B.7)}$$

the roots of which are $-a_1$, a_2 and hence the steady state is **unstable.**

For solving of (B. 6), we get

$$U_1 = U_{10}\, e^{-a_1 t} + \frac{U_{20}\, a_1\, a_{12}}{a_{11}\,(a_1 + a_2)}\,[\, e^{-a_1 t} - e^{a_2 t}\,]; \quad U_2 = U_{20}\, e^{a_2 t} \qquad \text{(B. 8)}$$

The solution curves are illustrated in figures (6) and (7) and the observations are presented in **TABLE- 2**

TABLE – 2

$U_{10} > U_{20}$	the Ammensal (N_1) while declining all throughout, dominates over the enemy(N_2) up to the time -instant $t^* = \frac{1}{(a_1 + a_2)} \log\left(\frac{U_{10}(a_1+a_2)a_{11}+a_1a_{12}U_{20}}{U_{20}((a_1+a_2)a_{11}+a_2a_{12})}\right)$ there after the dominance is reversed.- Fig(6).
$U_{10} < U_{20}$	The enemy (N_2) dominates over the Ammensal (N_1) all throughout. -Fig. (7).

Trajectories of Perturbed Species:

The trajectories (solution curves of (B. 6)) in $U_1 - U_2$ plane are given by

$$x + Py = (1+P)\ y^{-\frac{a_1}{a_2}} \qquad \text{(B. 9)}$$

where $x = \frac{U_1}{U_{10}}$, $y = \frac{U_2}{U_{20}}$ and $P = \frac{a_1\, a_2\, u_{20}}{a_{11}(a_1 + a_2)U_{10}}$

and are shown in Fig (8)

C).THE DEATH RATE OF ENEMY SPECIES IS GREATER THAN ITS BIRTH RATE.

Equation for the growth rate of the Ammensal species (S_1)

$$\frac{dN_1}{dt} = a_1 N_1 - a_{11} N_1^2 - a_{12} N_1 N_2 \qquad \text{(C.1)}$$

Equation for the growth rate of enemy species (S_2)

$$\frac{dN_2}{dt} = -a_2 N_2 \qquad \text{(C.2)}$$

The system has only two equilibrium states defined by

$$\frac{dN_1}{dt} = 0, \quad \frac{dN_2}{dt} = 0. \qquad \text{(C.3)}$$

The equilibrium points are obtained as

$E_1^{(II)}$: $\bar{N}_1 = 0$; $\bar{N}_2 = 0$ [Fully washed out state]

$E_2^{(II)}$: $\bar{N}_1 = \frac{a_1}{a_{11}}$; $\bar{N}_2 = 0$ [The Ammensal survives and enemies are washed out.]

4.1 Stability of the Equilibrium State $E_1^{(II)}$.

The corresponding linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= a_1 U_1, \\ \frac{dU_2}{dt} &= -a_2 U_2 \end{aligned}\right\} \qquad \text{(C.4)}$$

The characteristic equation for this system is

$$(\lambda - a_1)(\lambda + a_2) = 0 \qquad \text{(C.5)}$$

the roots of which are $a_1, -a_2$ and hence the steady state is **unstable.**

By solving (4.4) we get

$$U_1 = U_{10}\ e^{a_1 t}; \quad U_2 = U_{20}\ e^{-a_2 t} \qquad \text{(C.6)}$$

The solution curves are illustrated in Fig. (9) and (10) and the observations are presented in **TABLE- 3**

TABLE – 3

$U_{10} < U_{20}$	The enemy (N_2) while declining, dominates over the the Ammensal (N_1) up to the time -instant t*= $\frac{1}{(a_1 + a_2)} \log\left(\frac{U_{20}}{U_{10}}\right)$ there after the Ammensal (N_1) dominates over the enemy (N_2) and the enemy (N_2) declines further. -Fig (9).
$U_{10} > U_{20}$	The Ammensal (N_1) dominates over the the enemy (N_2). The enemy (N_2) declines all throughout.-Fig (10).

Trajectories of Perturbed Species: The trajectories (solution curves of (C.4)) in $U_1 - U_2$ plane are given by

$$x^{a_2} y^{a_1} = 1 \tag{C.7}$$

where $x = \frac{U_1}{U_{10}}$, $y = \frac{U_2}{U_{20}}$

as shown in Fig (8)

4.2 Stability of the Equilibrium State $E_2^{(II)}$.

The corresponding linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= -a_1 U_1 - \frac{a_1 a_{12}}{a_{11}} U_2 , \\ \frac{dU_2}{dt} &= -a_2 U_2 \end{aligned}\right\} \tag{C.8}$$

The characteristic equation for this system is

$$(\lambda + a_1)(\lambda + a_2) = 0 \tag{C.9}$$

the roots of which are $-a_1, -a_2$ i.e. both the roots are negative,

Hence the steady state is **stable**.

Also by solving (C.8), we get

$$U_1 = U_{10}\, e^{-a_1 t} + \frac{U_{20}\, a_1\, a_{12}}{a_{11}(a_1 + a_2)} \left[e^{-a_1 t} - e^{-a_2 t} \right]; \quad U_2 = U_{20}\, e^{-a_2 t} \tag{C.10}$$

The solution curves are illustrated in Fig (11) and (12); the conclusions are presented in **TABLE- 4**.

TABLE- 4

$U_{10} < U_{20}$	the enemy (N2) continuous to dominate over the Ammensal (N1) and both the species converge asymptotically to the equilibrium point. -Fig(11)
$U_{10} > U_{20}$	the Ammensal (N_1) while declining all throughout, dominates over the enemy(N_2) up to the time -instant $t^* = \frac{1}{(a_1 - a_2)} \log\left(\frac{U_{10}(a_1-a_2)a_{11}+a_1 a_{12} U_{20}}{U_{20}((a_1-a_2)a_{11}+a_2 a_{12}))}\right)$ there after the enemy (N_2) dominates over the Ammensal (N_1) .-Fig(12).

Trajectories of Perturbed Species:

The trajectories (solution curves of (C.8)) in $U_1 - U_2$ plane are given by

$$x + Py = (1+P)\, y^{\frac{a_1}{a_2}} \tag{C.11}$$

where $x = \frac{U_1}{U_{10}}$, $y = \frac{U_2}{U_{20}}$ and are shown in Fig (13)

II) the Ammensal species (S_1) with unlimited resources and the enemy species(S_2) with limited resources

This is the case with $k_1 \rightarrow \infty$ and $k_2 < \infty$ i.e., when $a_{11}=0$ and $a22 \neq 0$

D)Basic equation for the growth rate of the Ammensal species (S_1)

$$\frac{dN_1}{dt} = a_1 N_1 - a_{12} N_1 N_2 \tag{D.1}$$

Basic equation for the growth rate of enemy species (S_2)

$$\frac{dN_2}{dt} = a_2 N_2 - a_{22} N_2^2 \tag{D.2}$$

The system has only two equilibrium states defined by

$$\frac{dN_1}{dt} = 0\,, \quad \frac{dN_2}{dt} = 0\,. \qquad \text{(D.3)}$$

The equilibrium points are obtained as

$E_1^{(III)}$: $\bar{N}_1 = 0$; $\bar{N}_2 = 0$ [Fully washed out state]

$E_2^{(III)}$: $\bar{N}_1 = 0$; $\bar{N}_2 = \frac{a_2}{a_{22}}$ [The enemy survives and the Ammensals are washed out]

<u>THE STABILITY OF THE EQUILIBRIUM STATES</u>

E)The Stability of the Equilibrium State $E_1^{(III)}$.

The corresponding linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= a_1 U_1 \\ \frac{dU_2}{dt} &= a_2 U_2 \end{aligned}\right\} \qquad \text{(E.1)}$$

It becomes as (B.2); hence we get the results as in (B.2).

6.2 The Stability of the Equilibrium State $E_2^{(III)}$.

The corresponding Linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= a_1 U_1 - \frac{a_2 a_{12}}{a_{22}} U_1, \\ \frac{dU_2}{dt} &= -a_2 U_2 \end{aligned}\right\} \qquad \text{(E.2)}$$

the characteristic equation for which is

$$\left(\lambda - \left(\frac{a_1 a_{22} - a_2 a_{12}}{a_{22}}\right)\right)\left(\lambda + a_2\right) = 0 \qquad \text{(E.3)}$$

The roots of this equation are $\frac{a_1 a_{22} - a_2 a_{12}}{a_{22}}$; $-a_2$;

Case (1): if $\frac{a_1}{a_{12}} > \frac{a_2}{a_{22}}$

one of the two roots is positive. Hence the steady state is **unstable.**

We have obtained the solution as

$$U_1 = U_{10}\ e^{\left(\frac{a_1 a_{22} - a_2 a_{12}}{a_{22}}\right)t} \quad ; \quad U_2 = U_{20}\ e^{-a_2 t} \qquad \text{(E.4)}$$

the solution curves are illustrated in Fig (9) and (10) and the conclusions are presented in **TABLE-5.**

Case (2): If $\frac{a_1}{a_{12}} < \frac{a_2}{a_{22}}$

both the roots are negative, Hence the steady state is **stable**.

We have obtained the solution as

$$U_1 = U_{10}\ e^{\left(\frac{a_1 a_{22} - a_2 a_{12}}{a_{22}}\right)t} \quad ; \quad U_2 = U_{20}\ e^{-a_2 t}. \qquad \text{(E.5)}$$

The solution curves are illustrated in Fig (15) and (16) .The conclusions are presented in **TABLE-5.**

Trajectories of Perturbed species:

The trajectories (solutions curves of E.2) in $U_1 - U_2$ plane are given

by $\left(\frac{U_1}{U_{10}}\right)^{\frac{a_{22}}{a_1 a_{22} - a_2 a_{12}}} . \left(\frac{U_2}{U_{20}}\right)^{1/a_2} = 1$; Let P= $\frac{a_{22}}{a_1 a_{22} - a_2 a_{12}}$ and are shown in Fig (8) of (E.4) and Fig (14) of (E.5) (E.6)

TABLE- 5

	If $\frac{a_1}{a_{12}} > \frac{a_2}{a_{22}}$	If $\frac{a_1}{a_{12}} < \frac{a_2}{a_{22}}$
$U_{10} < U_{20}$	The declining enemy (N_2) dominates over the flourishing Ammensal (N_1) up to the time instant $t^* = \frac{a_{22}}{(a_1+a_2)a_{22} - a_2 a_{12}} \log\left(\frac{U_{20}}{U_{10}}\right)$ after that the dominance is reversed. -Fig (9).	Both N1 and N2 decline. The enemy(N_2) dominates over the Ammensal (N_1) up to the time -instant $t^* = \frac{a_{22}}{(a_1+a_2)a_{22} - a_2 a_{12}} \log\left(\frac{U_{20}}{U_{10}}\right)$ only.- Fig(15)
$U_{10} > U_{20}$	The Ammansal(N_1) flourishes and the enemy(N_2) declines.-Fig(10).	Both the species decline throughout asymptotically approaching the equilibrium point. However the Ammensal(N_1) dominates over the enemy (N_2) .- Fig(16)

F).THE DEATH RATE OF BOTH SPECIES IS GREATER THAN THEIR BIRTH RATE.

Equation for the growth rate of the Ammensal species (S_1)

$$\frac{dN_1}{dt} = -a_1 N_1 - a_{12} N_1 N_2 \tag{F.1}$$

Equation for the growth rate of enemy species (S_2)

$$\frac{dN_2}{dt} = -a_2 N_2 - a_{22} N_2^2$$

The equilibrium point is obtained as $\bar{N}_1 = 0;\ \bar{N}_2 = 0$ (F.2)

The corresponding linearised perturbed equations are

$$\left.\begin{aligned} \frac{dU_1}{dt} &= -a_1 U_1 \quad , \\ \frac{dU_2}{dt} &= -a_2 U_2 \end{aligned}\right\} \tag{F.3}$$

It becomes as (4.4); hence we get the results as in (4.4).

It is also observed that these two models are stable when the death rate is greater than the birth rate for both the species at fully washed out state.

The corresponding linearised perturbed equations are

$$\frac{dU_1}{dt} = -\ a_1 U_1, \quad \frac{dU_2}{dt} = -\, a_2 U_2 \qquad \text{(F.4)}$$

The characteristic equation for this system is $(\lambda + a_1)(\lambda + a_2) = 0$ (F.5)

the roots of which are $-a_1, -a_2$. i.e. both the roots are negative, i.e.

Hence the steady state is **stable**.

For solving of (F.3), we get $U_1 = U_{10}\ e^{-a_1 t}$; $U_2 = U_{20}\ e^{-a_2 t}$

The solution curves are illustrated as above.

G) COMPARISIONS BETWEEN THESE TWO MODELS WITH LIMITED RESOURCES

<table>
<tr><th>Equilibrium states</th><th>S_1(LIMITED)
S_2 (LIMITED)</th><th>S_1 (LIMITED)
S_2 (UNLIMITED)</th><th>S_1 (UNLIMITED)
S_2 (LIMITED)</th></tr>
<tr><td rowspan="2">Fully washed out state
$[\bar{N}_1 = 0;\ \bar{N}_2 = 0]$</td><td rowspan="2">unstable</td><td>unstable
(Also in the case of death rate $>$ birth rate of N_2 species)</td><td>unstable
(Also in the case of death rate $>$ birth rate of N_2 species)</td></tr>
<tr><td>stable
(in the case of death rate $>$ birthrate of the both species)</td><td>stable
(in the case of death rate $>$ birth rate of both species)</td></tr>
<tr><td rowspan="2">The enemy survives and the Ammensal is washed out state
$[\bar{N}_1 = 0;\ \bar{N}_2 = \frac{a_2}{a_{22}}]$</td><td>unstable
if $\frac{a_1}{a_{12}} > \frac{a_2}{a_{22}}$</td><td rowspan="2">Does not exit</td><td>unstable
if $\frac{a_1}{a_{12}} > \frac{a_2}{a_{22}}$</td></tr>
<tr><td>stable
if $\frac{a_1}{a_{12}} < \frac{a_2}{a_{22}}$</td><td>stable
if $\frac{a_1}{a_{12}} < \frac{a_2}{a_{22}}$</td></tr>
</table>

<table>
<tr><td rowspan="2">The Ammensal survives and enemy is washed out state.
[$\bar{N}_1 = \frac{a_1}{a_{11}}$; $\bar{N}_2 = 0$]</td><td rowspan="2">unstable</td><td>unstable</td><td rowspan="2">Does not exit</td></tr>
<tr><td>stable
(in the case of death rate > birth rate of N_2 species)</td></tr>
<tr><td>The co-existent state
[$\bar{N}_1 = \frac{a_1 a_{22} - a_2 a_{12}}{a_{11}\, a_{22}}$;
$\bar{N}_2 = \frac{a_2}{a_{22}}$]</td><td>stable</td><td>Does not exit</td><td>Does not exit</td></tr>
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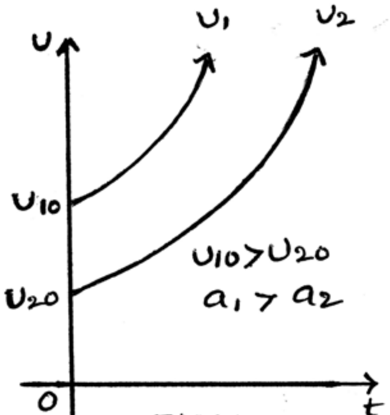
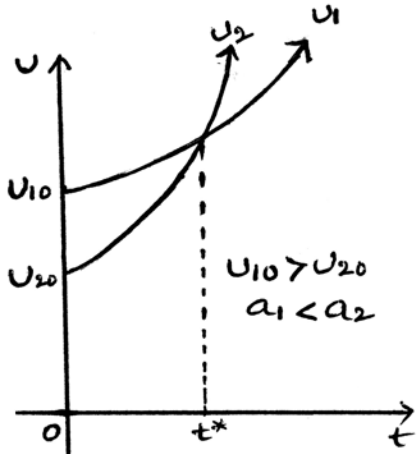
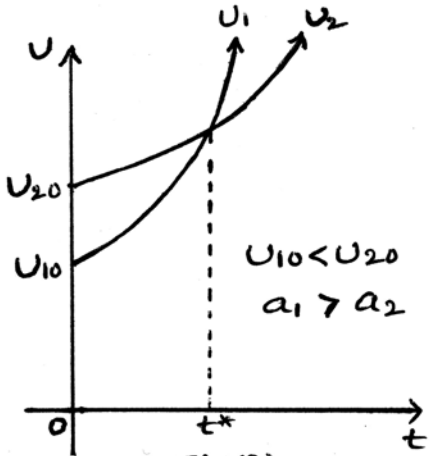
FIGURES



Fig(1)



Fig(2)



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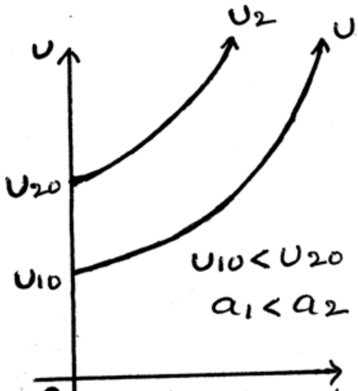

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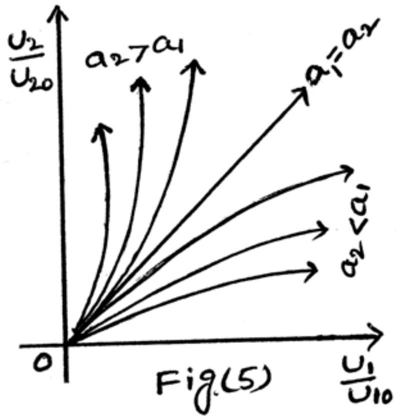

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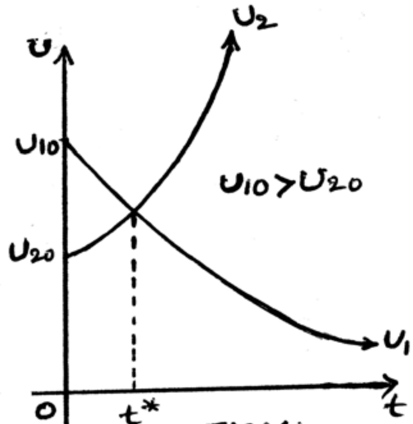
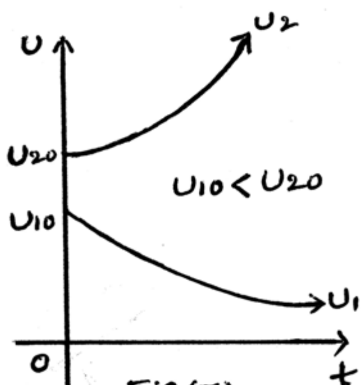
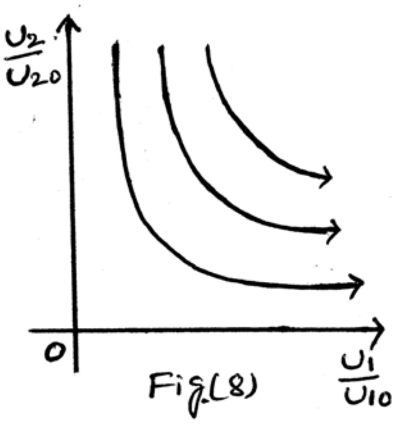


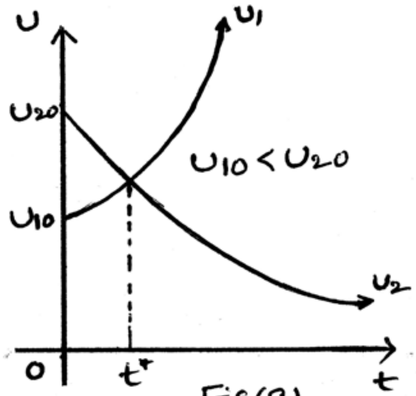
Fig(6)



Fig(7)



Fig(8)



Fig(9)

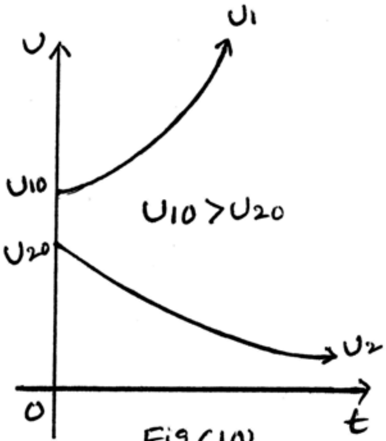


Fig.(10)

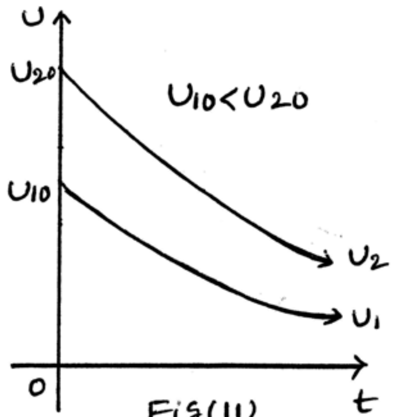


Fig.(11)

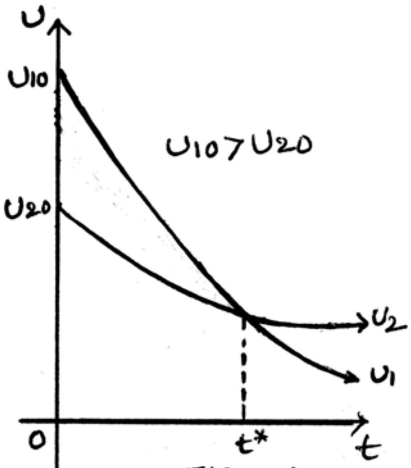


Fig.(12)

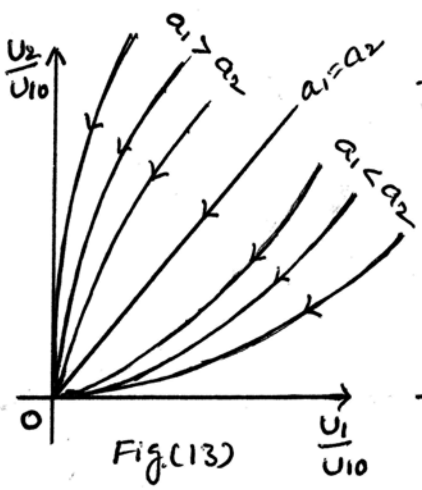


Fig.(13)

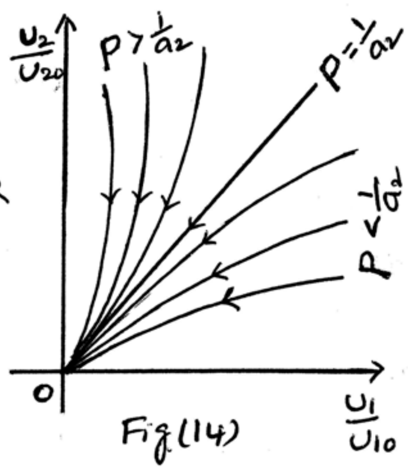


Fig.(14)

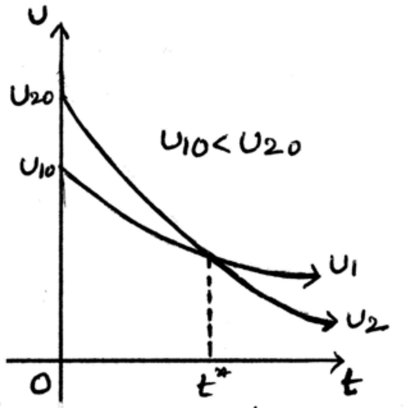


Fig.(15)

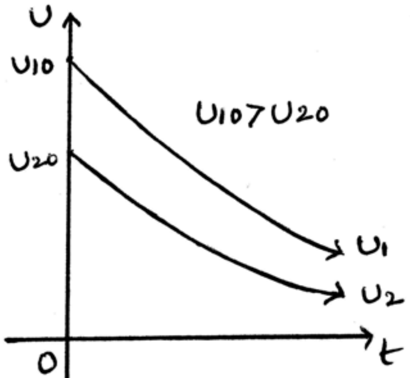


Fig.(16)

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