Analysis of translocatory balance in durian (*Durio zibethinus*) fruit

KAZUHARU OGAWA,[1] AKIO FURUKAWA,[2] AHMAD MAKMOM ABDULLAH[3] and
MUHAMAD AWANG[3]

[1] *Section of Forest Ecophysiology, School of Agricultural Sciences, Nagoya University, Chikusa-Ku, Nagoya 464-01, Japan*

[2] *Environmental Biology Division, The National Institute for Environmental Studies, Tsukuba, Ibaraki 305, Japan*

[3] *Department of Environmental Sciences, Universiti Pertanian Malaysia, 43400 UPM Serdang, Malaysia*

Summary   We estimated translocatory balance in fruit of the tropical tree *Durio zibethinus* Murray on the basis of a compartment model. Rates of fruit respiration, dry weight growth and translocation increased with time. Over the 8.2-weeks of fruit development, the relative distribution of translocation was 80% to dry weight growth and 20% to respiration. The ratio of respiration rate to translocation rate, which ranged from 14 to 32%, tended to decrease with time, whereas the ratio of dry weight growth rate to translocation rate, which ranged from 68 to 86%, tended to increase with time. The relationship between dry weight growth rate and translocation rate was fitted by a power function, where dry weight growth rate was statistically proportional to translocation rate. The relationship between respiration rate and translocation rate was formulated by a smooth curve, where respiration rate increased as translocation rate increased. Examination of these ratios with respect to the translocation rate indicated that the dry weight growth rate/translocation rate ratio increased slightly with increasing translocation rate, whereas the respiration rate/translocation rate ratio decreased with increasing translocation rate. A comparative analysis of these results with those obtained for *Cinnamomum camphora* (L.) J. Presl revealed a lower ratio of translocation to dry weight growth in *D. zibethinus* than in *C. camphora*, indicating that *D. zibethinus* fruits have a low translocatory efficiency.

Keywords: compartment model, dry weight growth, fruit respiration, translocation, translocatory efficiency.

Introduction

Most studies of CO_2 exchange during the fruiting process of woody plants growing in arctic (Linder and Troeng 1981, Koppel et al. 1987), temperate (Dickmann and Kozlowski 1970, Rook and Sweet 1971, Jones 1981, Ogawa et al. 1988, Takano and Ogawa 1993), and tropical regions (Whiley et al. 1992, Ogawa et al. 1995) have focused on the carbon requirement of fruits. Little is known about translocation into fruits from other parts of the tree (Harper 1977). Takano and Ogawa (1993) developed a compartment model to estimate transloca-

tion into a fruit and used it to analyze the translocatory balance of the fruit of the temperate tree *Cinnamomum camphora* (L.) J. Persl.

We have used a modification of the translocatory model described by Takano and Ogawa (1993) to estimate the translocatory balance of fruit of the tropical tree durian (*Durio zibethinus* Murray). We compared the estimated translocatory balance for *D. zibethinus* fruit with the results obtained by Takano and Ogawa (1993) for *C. camphora* fruit to determine species-specific differences in translocation.

Materials and methods

Research site

The study was conducted on two trees (Trees 1 and 2) of *D. zibethinus* growing in an experimental field station of Universiti Pertanian Malaysia (UPM) in Selangor, Malaysia. The stem diameters at breast height of Trees 1 and 2 were 27.4 and 34.1 cm, respectively.

Modeling

Takano and Ogawa (1993) developed a compartment model to estimate the translocatory balance of the fruiting process in woody plants, based on the principles for estimating translocation in leaves outlined by Hozumi and Kurachi (1991). We have modified the model of Takano and Ogawa (1993) by including variables for daytime and nighttime dark respiration before fruit fall or death (Figure 1). In the modified model, net translocation into a fruit (ΔT_r, g_{DW} fruit^{-1}) over a given time
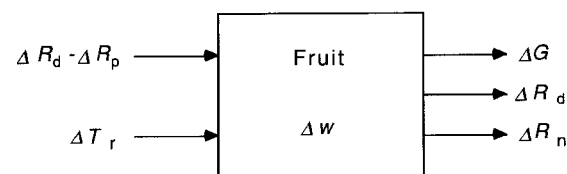

Figure 1. Compartment model of translocatory balance in a fruit before fruit fall or death.

interval (Δt, weeks) is expressed as (Hozumi and Kurachi 1991):

$$\Delta T_r = \Delta R_d + \Delta R_n - (\Delta R_d - \Delta R_p) + \Delta w + \Delta G$$
$$= \Delta R + \Delta w + \Delta G, \tag{1}$$

where ΔR_d is daytime dark respiration, ΔR_n is nighttime dark respiration, ΔR is the sum of ΔR_n and ΔR_p, ΔR_p is daytime net respiration, $(\Delta R_d - \Delta R_p)$ represents photosynthetic CO_2 refixation (Linder and Troeng 1981, Koppel et al. 1987), Δw is dry weight growth, and ΔG is grazing. If ΔG is negligible, then Equation 1 simplifies to:

$$\Delta T_r = \Delta R + \Delta w. \tag{2}$$

Estimation of translocatory balance

In situ CO_2 exchange of fruits was measured continuously with an open gas exchange system (Ogawa et al. 1995). The measurements were performed on three individual fruits on Tree 1 in October 1992 and Tree 2 in September and October 1993. Daytime dark respiration was measured by covering the assimilation chamber with aluminum foil.

Dry weights of sample fruits (w, g_{DW} fruit^{-1}) were estimated from: $w = 0.105(D_S D_L)^{1.45}$, where D_S and D_L are the lateral and longitudinal diameters (cm) of fruits ($n = 192$, $r^2 = 0.99$), respectively.

The rates of development of six fruits were estimated based on the assumption that differences in the estimated dry weights of sample fruits were equivalent to the differences in time (t, weeks) of the logistic growth equation, where $w = 634.3/(1 + 15.9 \exp(-0.548t))$ ($r^2 = 1.00$). The logistic equation was constructed from the mean dry weights of 18 attached fruits of Tree 2. We then used Equation 2 and the data obtained for CO_2 exchange, fruit dry weight and fruit development to calculate the values of the variables affecting translocatory balance. The dry matter/CO_2 conversion factor was assumed to be 0.614 ($C_6H_{10}O_5/6\ CO_2$) (Mariko and Koizumi 1970, Yoda 1993).

Results

Time courses of respiration, dry weight growth and translocation rates

The estimated rates of respiration, dry weight growth and translocation, which increased with time, attained maximum values of 23.4, 85.5 and 108.0 g_{DW} fruit^{-1} week^{-1}, respectively (Figure 2). The ratio of respiration to net translocation ($\Delta R/\Delta T_r$), which ranged from 14 to 32%, tended to decrease with time, whereas the ratio of dry weight growth to net translocation ($\Delta w/\Delta T_r$), which ranged from 68 to 86%, tended to increase with time. The percentage of daytime net respiration to respiration ($\Delta R_p/\Delta R$), which ranged from 59 to 67%, tended to decrease slightly with time.

At Weeks 2.9 and 6.6 (Figure 2), photosynthetic refixation of CO_2 ($\Delta R_d - \Delta R_p$ or $(\Delta R_d - \Delta R_p)/(\Delta R_d + \Delta R_n)$) (Linder and Troeng 1981, Koppel et al. 1987) was 6.4 and 9.2 g_{DW} fruit^{-1}
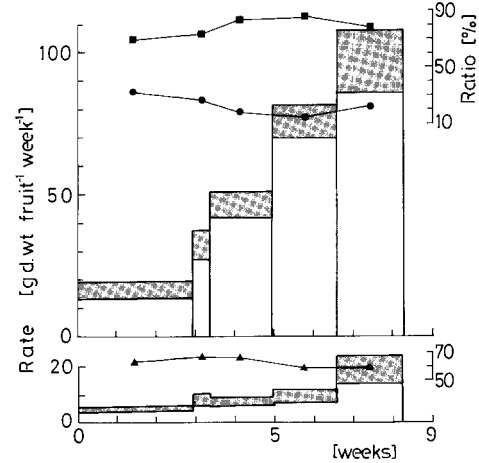

Figure 2. Time course of translocatory balance estimated from Equation 2. Upper panel: rates of respiration ($\Delta R/\Delta t$, shaded), dry weight growth ($\Delta w/\Delta t$, unshaded) and translocation ($\Delta T_r/\Delta t$), and ratios of respiration to net translocation ($\Delta R/\Delta T_r$, ●) and dry weight growth to net translocation ($\Delta w/\Delta T_r$, ■). Lower panel: rates of nighttime respiration ($\Delta R_n/\Delta t$, shaded) and daylight net respiration ($\Delta R_p/\Delta t$, unshaded) (Linder and Troeng 1981, Koppel et al. 1987), and ratio of daylight net respiration to respiration ($\Delta R_p/\Delta R$, ▲).

week^{-1} or 24 and 23% of daily dark respiration ($\Delta R_d + \Delta R_n$), respectively.

Translocatory balance over the entire 8.2-week estimation period

Estimated total amounts of respiration and dry weight growth were 94.5 and 373.4 g_{DW} fruit^{-1}, respectively, giving a total translocation of 467.9 g_{DW} fruit^{-1} over the 8.2-week period. The relative distributions of translocation were 80% to dry weight growth and 20% to respiration, of which 61% was allocated to daytime net respiration.

Relationships between rates of dry weight growth and respiration, and translocation rate

The relationship between dry weight growth rate and translocation rate was approximated by a power function (Figure 3):

$$\Delta w/\Delta t = a(\Delta T_r/\Delta t)^b, \tag{3}$$

where a and b are coefficients with values of 0.511 g_{DW}^{1-b} fruit^{b-1} week^{b-1} and 1.106 ± 0.46 (SE), respectively. Because the value of b did not significantly differ from unity at $P = 0.01$, dry weight growth rate was statistically proportional to translocation rate.

From Equations 2 and 3, the relationship between respiration rate and translocation rate can be expressed as:

$$\Delta R/\Delta t = \Delta T_r/\Delta t - a(\Delta T_r/\Delta t)^b, \tag{4}$$

where respiration rate increases as the translocation rate increases (Figure 3), as predicted by Equation 2.

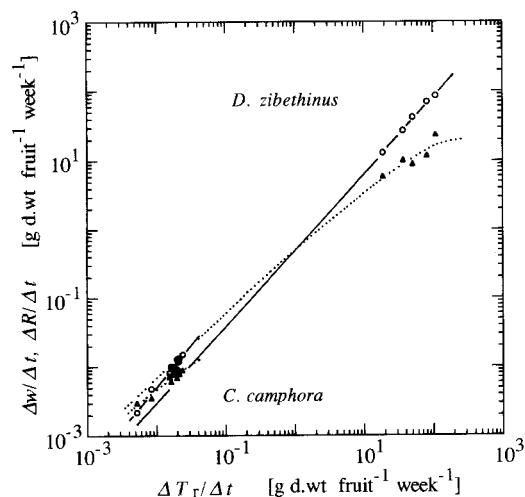By transforming Equations 3 and 4, the relationships be-

Figure 3. Relationships of dry weight growth rate ($\Delta w/\Delta t$, ○) and respiration rate ($\Delta R/\Delta t$, ▲) to translocation rate ($\Delta T_r/\Delta t$) in *Durio zibethinus* and *Cinnamomum camphora* (Takano and Ogawa 1993). The solid lines and dotted smooth curves describe Equations 3 and 4, respectively. The determination coefficient of Equation 3 is 0.99 in *D. zibethinus* and 0.98 in *C. camphora*.

tween the $\Delta w/\Delta T_r$ and $\Delta R/\Delta T_r$ ratios and translocation rate are given by:

$$\Delta w/\Delta T_r = a(\Delta T_r/\Delta t)^{b-1} \tag{5}$$

$$\Delta R/\Delta T_r = 1 - a(\Delta T_r/\Delta t)^{b-1}. \tag{6}$$

The ratio of $\Delta w/\Delta T_r$ increased slightly as the translocation rate increased, whereas the ratio of $\Delta R/\Delta T_r$ decreased as the translocation rate increased (Figure 4).

Discussion

Species differences in translocatory balance

Takano and Ogawa (1993) investigated the seasonal variation of translocatory balance during the development of fruits of *C. camphora* growing in the temperate zone. They demonstrated that the ratio of dry weight growth to translocation
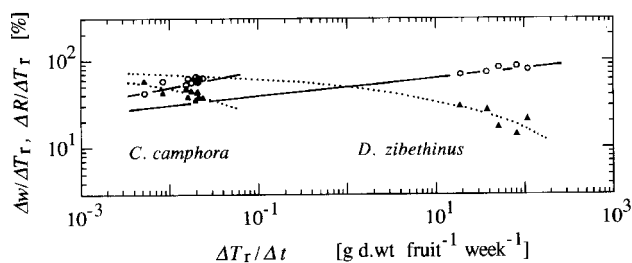

Figure 4. Relationships of the dry weight/net translocation ($\Delta w/\Delta T_r$, ○) and respiration/net translocation ($\Delta R/\Delta T_r$, ▲) ratios to translocation rate ($\Delta T_r/\Delta t$) in *Durio zibethinus* and *Cinnamomum camphora* (Takano and Ogawa 1993). The solid straight lines and dotted smooth curves describe Equations 5 and 6, respectively.

ranged from 43 to 62%, which is less than the range of 68 to 86% that we observed for *D. zibethinus* fruit. We estimated that the ratio for the entire 8.2-week study period was 80%, which is slightly higher than published values for an entire growing season, e.g., 67% for *Pinus sylvestris* L. (Linder and Troeng 1981) and 60–64% for *Picea abies* (L.) Karst. (Koppel et al. 1987) in the arctic region, and 59% for *C. camphora* (Takano and Ogawa 1993) in the temperate region.

Translocatory balance

We compared our results and those for *C. camphora* (Takano and Ogawa 1993) based on the quantitative relationships of Equations 3–6. The coefficients a and b of the relationship between $\Delta w/\Delta t$ and $\Delta T_r/\Delta t$ (see Equation 3) were computed to be 1.323 g_{DW}^{1-b} fruit^{b-1} week^{b-1} and 1.202 ± 0.057, respectively, in *C. camphora* fruits. The value of b differed significantly from unity at $P = 0.01$ and was higher than in *D. zibethinus*, whereas the value of a was lower. The value of $\Delta w/\Delta t$ relative to $\Delta T_r/\Delta t$ in *D. zibethinus* was higher during the early stages of growth than in *C. camphora* (Figure 3), indicating that, during the early stages of fruit development, the dry weight growth rate is lower in *D. zibethinus* than in *C. camphora* at a specified translocation rate. The value of $\Delta R/\Delta t$ relative to $\Delta T_r/\Delta t$ (see Equation 4) in *D. zibethinus* was below that in *C. camphora*.

The value of $\Delta w/\Delta T_r$ relative to $\Delta T_r/\Delta t$ (see Equation 5) in *D. zibethinus* was below that in *C. camphora* (Figure 4), indicating that the dry weight growth rate at any specific translocation rate differs between the two species. In contrast, the value of $\Delta R/\Delta T_r$ relative to $\Delta T_r/\Delta t$ (see Equation 6) in *D. zibethinus* was higher than that in *C. camphora*.

Based on the relationships predicted by Equations 3–6, we conclude that the ratio of dry weight growth to translocation is lower in *D. zibethinus* than in *C. camphora*, whereas the ratio of respiration to translocation is higher in *D. zibethinus* than in *C. camphora*. The lower ratio of dry weight growth to translocation in *D. zibethinus* is indicative of a low translocatory efficiency in this species. We conclude that there are species-specific differences in the interrelationship among variables relating to translocatory balance.

References

Dickmann, D.E. and T.T. Kozlowski. 1970. Photosynthesis by rapidly expanding green strobili of *Pinus resinosa*. Life Sci. 9:549–552.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, 892 p.

Hozumi, K. and N. Kurachi. 1991. Estimation of seasonal changes in translocation rates in leaves of a Japanese larch stand. Bot. Mag. Tokyo 104:25–36.

Jones, H.G. 1981. Carbon dioxide exchange of developing apple (*Malus pumula* Mill.) fruits. J. Exp. Bot. 32:1203–1210.

Koppel, A., E. Troeng and S. Linder. 1987. Respiration and photosynthesis in cones of Norway spruce (*Picea abies* (L.) Karst.). Trees 1:123–128.

Linder, S. and E. Troeng. 1981. The seasonal course of respiration and photosynthesis in strobili of Scots pine. For. Sci. 27:267–276.

Mariko, S. and H. Koizumi. 1970. Respiration for maintenance and growth in *Reynoutria japonica* ecotypes from different altitudes on Mt. Fuji. Ecol. Res. 8:241–246.

Ogawa, K., A. Hagihara and K. Hozumi. 1988. Photosynthesis and respiration in cones of hinoki (*Chamaecyparis obtusa*). J. Jpn. For. Soc. 70:220–226.

Ogawa, K., A. Furukawa, A. Hagihara, A.A. Makmom and M. Awang. 1995. *In situ* CO_2 gas-exchange in fruits of a tropical tree, *Durio zibethinus* Murray. Trees 9:241–246.

Rook, D.A. and G.B. Sweet. 1971. Photosynthesis and photosynthate distribution in Douglas-fir strobili grafted to young seedlings. Can. J. Bot. 49:13–17.

Takano, Y. and K. Ogawa. 1993. Seasonal course of CO_2 gas-exchange in fruits of *Cinnamomum camphora. In* Abstracts of 104th Meeting of Jpn. For. Soc., Morioka, p 135 (in Japanese).

Whiley, A.W., B. Schaffer and S.P. Lara. 1992. Carbon dioxide exchange of developing avocado (*Persea americana* Mill.) fruit. Tree Physiol. 11:85–94.

Yoda, K. 1993. Community respiration in a lowland rain forest in Pasoh, Peninsular Malaysia. Jpn. J. Ecol. 33:183–197.