Photosynthetic Pathway and Biomass Energy Production

Adapted crop species permit the exploitation of tropical environments on the basis of rainfall.

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Plant scientists the world over share a major goal: to bring food production into balance with the world's population. Although the potential for production of many crops has increased as a result of advances in agricultural research, other limitations are becoming apparent, particularly as the cost of nitrogen fertilizers increases with the cost of methane and petroleum. The linkage of food and energy demonstrates a need to find new and to return the greatest yield of biomass energy per unit of energy input. In Brazil, where programs for converting plant biomass to ethanol are well advanced, the crops of choice for biomass production are sugarcane, sorghum, and cassava, all of which are well adapted to the warm tropics.

Programs are under way in Brazil to expand the areas planted with sugarcane and cassava, but both crops would re-

Summary. The current interest in locating new or alternative sources of energy has focused attention on solar energy capture by crops that can be subsequently utilized as a substitute for fossil fuels. The very high productivity of sugarcane and the fact that it accumulates sugars that are directly fermentable to alcohol may have caused seemingly less productive crops to be overlooked. We show here that recoverable alcohol from achievable commercial yields of pineapple can actually equal that of sugarcane, with the pineapple crop requiring only a fraction of the water used by sugarcane. Pineapple is well adapted to the subhumid or semiarid tropics and thus is particularly well suited for exploiting large areas not now under cultivation with any crop of commercial value.

inexpensive supplies of energy to supplement fossil fuel resources.

Solar biomass energy is considered to be a low-cost alternative to fossil fuels in areas of the tropics where fuel reserves or capital for resource development are scarce (1, 2). However, low soil fertility and the quantity and distribution of rainfall often limit crop productivity in large areas of the tropics (3). There is no substitute for fertilizer on soils low in plant nutrients, but the selection of crops that have good productivity and a low water requirement will increase the efficiency of biomass energy recovery.

The culture of many crops requires caloric inputs that equal or exceed the calories stored in commodities derived from the crop (4). Crops grown solely for fuel must yield more calories after processing than the caloric value of inputs required to produce them. Crops that are well adapted to their environment are likely

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quire supplemental irrigation to maxi mize productivity in the immense Cerrado of Brazil. Although pineapple is grown commercially in at least five states in Brazil and is reported to be well adapted to the ecological conditions of the Cerrado (5), to our knowledge it has not been considered as a crop that has potential for biomass production and conversion to alcohol, probably because it is generally thought to have low productivity in comparison with plants that are photosynthetically more efficient (6). However, pineapple has anatomical and morphological attributes that confer adaptational advantages to the crop when it is grown under conditions of limited water supply; furthermore, its productivity is higher than is generally recognized (7).

In this article we briefly review the environmental requirements and certain physiological characteristics of cassava, sugarcane, and pineapple. The quantities of fermentable substrate produced by these crops under optimum management are then presented. Finally, we contrast the alcohol production potential of the three crops per unit of water consumed, giving particular emphasis to pineapple, a crop that we believe has been overlooked in the search for adapted species that can contribute to the energy needs of countries in the tropics.

Environmental Requirements

The zone of sugarcane and pineapple production extends over a range of latitude greater than 60° centering on the equator (7, 8). Cassava production generally is concentrated in an area of about 15° on either side of the equator (9).

The length of the growing season for sugarcane varies from 10 months or less in Louisiana to 2 years or more in South Africa, Peru, and Hawaii. For pineapple, the growing period for the mother or plant crop requires about 14 months in equatorial areas but up to 3 years at extreme north and south latitudes. A second or ratoon crop of pineapple is often harvested from the same plant in about half of the time required to produce the plant crop. Cassava is commonly grown as an annual crop, but the roots store well in the soil and continue to accumulate starch for at least 21 months (10).

Water requirements differ for the three crops. Sugarcane has high water requirements as is demonstrated by the fact that in Hawaii cane is irrigated on lands that receive more than 2000 millimeters of annual rainfall, primarily because rainfall distribution is variable (11). Where cane is irrigated, water is applied at 1.0 to 1.25 times pan evaporation. In other canegrowing areas, yields generally would not be economically profitable without irrigation where rainfall is less than 2000 to 2250 mm annually (12). Although cassava is grown in areas where rainfall ranges from less than 1000 mm to 4000 mm (13), the water requirement for cassava is less than for sugarcane and the crop is more drought resistant. Though data are scarce, yields apparently fall if rainfall is much less than 1500 mm. Yields dropped from 26.4 to 18.1 tons per hectare as rainfall decreased from 1502 to 1162 mm per year (14). During severe drought, cassava leaves abscise, growth stops, and the plant becomes virtually dormant (15). When the dry period

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Table 1. The relative proportion of plant material displayed as leaves for cassava, sugarcane, and pineapple. The data for cassava are from (44), for sugarcane from (41), for pineapple from (46).

Time after planting (months)	Cassava	Sugarcane		Pineapple	
	leaves (percentage of plant dry weight)	Total plant fresh weight (g)	Percentage green top	Total plant dry weight (g)	Percentage leaves
3	16			64	83
6	22			96	88
9	8	249	32	296	90
12	2	434	21	551	88
14		433	18		
15	7			812	80
16.5		401	16		
18	7	390	15	1176	65
20		386	13	1278	47
21	1				

is over, starch reserves in the root are mobilized to produce a new leaf canopy.

Pineapple has a lower water requirement than either sugarcane or cassava. Optimum rainfall for pineapple growth is in the range 1000 to 1500 mm (16-18), although the crop has been grown in Guadeloupe where rainfall exceeded 3500 mm (19). Pineapple is well adapted to semiarid conditions (20), and good yields are obtained consistently on the islands of Molokai and Lanai, Hawaii, where rainfall may be as low as 600 mm (21). In areas where rainfall is less than 1000 mm (in such areas, potential evapotranspiration exceeds annual rainfall) and irrigation water is unavailable, good water management practices and uniform distribution of rainfall are required to obtain good vields. Pineapple is much more drought-tolerant than cassava and retains its leaves through extended dry periods. The survival and growth of pineapple during dry periods results from several factors. The array and shape of the leaves provide an efficient collection mechanism for light rains and dew (22). Anatomical features contributing to drought tolerance include few stomata, the presence of trichomes, a thick cuticle, and the presence of a water-storage tissue in the leaves. The water-storage tissue enables the plant to retain its leaves during times of drought so that carbon assimilation can quickly resume after water stress is relieved.

The temperature requirements for cassava, sugarcane, and pineapple are similar (7, 14, 23, 24). Cassava has limited potential in areas where mean annual temperature is below 20°C, and for optimum growth a mean annual temperature of 25°C or greater is required (9). Sugarcane growth is also retarded markedly at temperatures below 21°C and ceases entirely when soil temperature drops to 16° C (8). Optimum temperatures for pineapple root and leaf elongation are about 29° and 32° C, respectively (25), and optimum day and night temperatures for pineapple are about 30° and 20° C, respectively (26).

The soil requirements of pineapple, cassava, and sugarcane are similar. All three crops are relatively tolerant of soil pH values in the range of 4.5 to 5.5. They apparently also are tolerant of soluble aluminum and manganese at the concentrations these elements normally exist in some soils of the tropics where these crops are grown (27). High yields of cassava, pineapple, and sugarcane are only obtained by increasing soil nutrient status by the addition of fertilizers. In general, soil type and soil pH appear to be less important than the quality of management practiced during the growing of these crops.

Productivity and Efficiency of Water Use

Attributes of cassava, pineapple, and sugarcane which are associated with their carbon assimilation pathways and which are important from a productivity standpoint include the CO₂ exchange rate (CER; expressed as milligrams of CO₂ per square decimeter of leaf area per hour on a unit leaf area basis); the rate of consumptive use of water; the effects of temperature on carbon assimilation rates, growth, and development; and the partitioning of photosynthate between leaves and other plant parts. Cassava and sugarcane are termed C3 and C4 species, respectively, because the first product of photosynthesis of cassava is a 3-carbon acid (3-phosphoglycerate), whereas that of sugarcane is the 4-carbon acid oxaloacetate, though the first detectable in appreciable product amounts is primarily malate (28-30). Pineapple is termed a crassulacean acid metabolism (CAM) plant because it fixes CO_2 in darkness by a process similar to that in C_4 plants and accumulates massive amounts of malate. The malate is decarboxylated in light and the released CO_2 is refixed by the C_3 pathway (29, 31, 32). Salient features of the biochemistry of all three pathways have been reviewed (29, 33).

The maximum CER's attained by cassava, sugarcane, and pineapple differ greatly because of differences in their photosynthetic pathways. Although data for cassava are scarce, CER's of up to 40 have been reported (14, 24). The CER for sugarcane may reach 80, but varietal differences can be very large (34). The maximum CER's found for CAM plants are in the range of 8 to 10 (35), but the highest rates reported for pineapple are 3.5 to 4.0 (36, 37). Cassava and sugarcane assimilate CO2 only in the light, while pineapple assimilates 33 to 90 percent of the CO₂ it uses at night and loses little or no CO₂ at any time during the day or night (37). Total assimilation over a 24-hour period by a single attached pineapple leaf is about 50 mg of CO₂ per square decimeter of leaf area (37). Such rates are probably much below daily rates for sugarcane and cassava although, apparently, data are not available for these crops.

The efficiency of water use by crop plants is also determined primarily by the pattern or pathway of CO₂ assimilation. Plants having the C3 pathway, such as cassava, have a lower CO₂ assimilation rate than C₄ plants, such as sugarcane, because of an approximately fourfold greater mesophyll resistance (r_m) (38). Under conditions of optimum light, the CO_2 gradient from the air to the leaf is steeper for C₄ plants than for C₃ plants because of their lower $r_{\rm m}$ that enables them to fix more CO_2 at the same stomatal resistance value (r_s) . Mesophyll cell walls of plants are generally assumed to be saturated with water so that at comparable r_s values the rate of transpiration would be equal for the two plants. The net result is that C₄ plants assimilate more carbon per unit of water transpired than do C3 plants. The low CER of pineapple is due primarily to very high r_s values (39). During dark fixation of CO_2 , CAM plants have an r_m comparable to that of C4 plants, while at the same time the water vapor gradient from the leaf to the atmosphere is at its daily minimum because of the absence of a radiation load on the leaf and higher nighttime humidity levels. Thus CO₂ assimilation can occur with minimal transpiration and maximum water conservation in CAM plants. Transpiration

ratios (the ratio of units of water transpired per unit of dry matter accumulated) for the three groups of plants have been reported to be greater than 500 for C_3 plants, 150 to 500 for C_4 plants, and less than 100 for CAM plants (35, 40). The reason for the apparently lower water requirement of cassava than sugarcane in the field may be that cassava is generally grown with a lower level of management inputs than is sugarcane. This is because much cassava is grown as a subsistence food crop whereas cane is primarily an industrial crop.

Values for CER give some indication of the potential crop growth rate (expressed as grams of dry matter per square meter of land area per day) (41), but partitioning of dry matter between leaves and other plant parts and leaf area duration can be more important than the CER (14, 34, 42, 43).

The relation between the CER and dry matter production has been examined for sugarcane (34), and some data are available for cassava (24, 44) but not for pineapple. Generally, the very high CER possessed by some sugarcane and cassava cultivars did not translate into a greater yield (24, 34). One possible reason for the poor correlation between CER and crop growth rate for sugarcane is that the very high CER's measured for some cultivars were not sustained for long periods of time (23).

Although CER's do not determine rates of dry matter production for sugarcane and cassava, crop growth rates for the two crops do correspond to their average rates of photosynthesis, and similar results have been reported for other C_3 and C_4 species (41). Crop growth rates for cassava are between 10 and 12.5 g per square meter per day (45), although values of 20 were reached if shed leaves were added. Rates as high as 50 have been reported for sugarcane. The highest reported for pineapple was 15, and that rate was sustained for more than 250 days (7). This high rate is in striking contrast to the low CER of a pineapple leaf. Leaf area partitioning and a low but sustained CER are at least partial explanations for the result. A much higher proportion of the total plant weight of pineapple is represented by leaf (46) than for either cassava (44) or sugarcane (47) (Table 1), and the high ratio of leaf to plant mass is sustained for more than a year. Optimum leaf indexes (LAI; expressed as square meters of leaf area per square meter of land area) for cassava and sugarcane are much smaller than for pineapple. Optimum LAI values for maximum cassava root yields were 3.0 to 3.5 (14) and LAI values of sugarcane 10 AUGUST 1979

Table 2. Energy expended in the agricultural production of pineapple (58).

Input	Energy expended* (Mcal ha ⁻¹ month ⁻¹)		
Manual labor	14.5		
Machines	49.0		
Fuels	542.6		
Fertilizers	338.9		
Insecticide plus herbicide	18.9		
Total	963.9		

*Energy expended for plant crop plus ratoon crop.

Table 3.	Sugar and	d starch	content	of	pine
apple frui	it and plan	t stem.			

Plant part	Sugar (g/plant)*	Starch (g/plant)
Fruit flesh	287.98	0.01*
Fruit shell and core	95.08	0.08*
Stem	16.54	189.10†

*Plant crop fruit or stem, 654 days after planting [from (46)]. †Plant crop and ratoon crop stem [from (53)].

were reported to range from 4 to 7 (11). Normal LAI values for pineapple reach or exceed 10 for periods of over 250 days (7, 48). The maintenance of very high LAI's permits pineapple to overcome much of the deficiency imposed by low CER. Furthermore, the consumptive use of water by pineapple actually declines as the LAI increases because a large nontranspiring leaf area intercepts proportionately more energy than a small leaf area, thus reducing the energy available to evaporate water from the soil (22).

The low rate of consumptive water use by the pineapple canopy permits its cultivation in areas where average annual rainfall is too low to obtain satisfactory yields of cassava or sugarcane without supplemental irrigation.

Energy Requirements for Production

Energy requirements for the production of cassava (49, 50) and for sugarcane with high levels of inputs are available,

but no data have been published for pineapple. To determine if a favorable energy balance exists for pineapple under a high level of management, we computed the energy costs for the production of the crop in Hawaii (Table 2). We assume that any management system that utilizes levels of inputs lower than are used in Hawaii will have a more favorable energy balance as was shown to be the case for sugarcane (49).

Fermentable Substrate and

Alcohol Production

Cassava and sugarcane are good candidates for alcohol production because of their potentially high productivity and because they accumulate large amounts of starch or sucrose. Sucrose can be fermented without pretreatment, but a preliminary degradation step is needed for starch. Sucrose levels in sugarcane stalks are low during rapid vegetative growth, but ripening of the plant with chemicals (23) or by withholding nitrogen and water (51) results in sucrose accumulation to concentrations of 15 to 20 percent. Starch accumulation by cassava roots continues over a period of several months, eventually reaching a level of about 33 percent on a fresh weight basis.

Sucrose and reducing sugars accumulate in pineapple fruit to a concentration of about 16 percent (Table 3) (52). The plant and ratoon crop stems also contain 30 to 40 percent starch on a dry weight basis a short while after the ratoon crop fruit has been harvested (53), so that both sugar and starch substrates are obtainable from pineapple.

Ideally, a comparison of yields and alcohol production potentials of different crops would utilize data obtained for a range of conditions. However, because of insufficient data, we have compared yields of sugarcane (Table 4) and pineapple (Table 5) grown under a high level of management in Hawaii with cassava yields (Table 6) from experimental plots in Costa Rica and Jamaica. Higher yields of all three crops have been obtained,

Table 4. Sugar production by sugarcane. The sugarcane was from fields ranging from 130 to 280 acres in different locations in Maui (59).

Location	Period (years)	Number of harvests	Age (months)	Sugar production (tons ha ⁻¹ month ⁻¹)
Kihei	1951 to 1957	4	24.2	1.15
Spreckelsville	1951 to 1957	4	23.7	1.18
Pulehu	1949 to 1957	5	24.2	1.31
Paia	1950 to 1956	5	23.9	1.20
Average			24.0	1.21

but we believe the data used here reflect readily attainable yields under good management. The usual crop cycles do not permit a direct comparison of yields of cassava, sugarcane, and pineapple. As discussed earlier, the period of growth for sugarcane ranges from 9 months to more than 24 months; for cassava about 10 months; and for a pineapple plant crop from 14 to 36 months with a ratoon crop requiring about half of the growing time required for a plant crop. In Hawaii, the plant crop is normally harvested 20 to 24 months after planting. For purposes of comparison, yields for the three crops have been calculated in terms of tons of sugar or starch per hectare per month, a common practice in the technical literature for sugarcane and sugarbeet.

Tables 4 to 6 show that carbohydrate (sugar or starch, or both) production per hectare per month for the three crops decreased in the order pineapple \geq sugarcane > cassava. Sugar production by the pineapple plant crop is almost half of that produced by the ratoon crop because the ratoon crop fruit is harvested about 1 year after the plant crop fruit. The pineapple fruit yield used for comparison here was 101 tons per hectare for the plant crop with a planting density of about 43,000 plants per hectare (46). Planting densities in Hawaii currently are about 10 percent higher than this and actual plantation yields may exceed 100 tons per hectare when growing conditions are optimum. We assumed a 20 percent reduction in vield for the ratoon crop but actual yields may be equal to the plant crop or much less depending on the quality of management and prevailing climate. The total starch yield from plant and ratoon crop stems was estimated at 6.7 tons per hectare (53), but the carbohydrate yield would be slightly higher because the stems also contain about 2.5 percent glucose on a dry weight basis (46, 52). The carbohydrate yield from pineapple stems is approximately equivalent to a cassava yield of 24.5 tons per hectare assuming a root starch content of 33 percent on a fresh weight basis.

As we mentioned at the outset, the recovery of calories from a crop must exceed the caloric value of inputs. Sugarcane yields approximately 25 calories of biomass energy or about 2 calories of digestible energy per calorie of input before processing (50). In Brazil, cassava yields about 6 calories per calorie of input prior to conversion to alcohol and about 1.2 calories after processing (49). For pineapple grown under intensive management in Hawaii, we calculate a

Table 5. Sugar and starch production by pineapple. The results are based on data in Table 3 and on a density of 43,000 plants per hectare.

Age (days)	Carbohydrate production $(tons ha^{-1} month^{-1})$		
	Sugar	Starch	
654	0.79		
365	1.15	0.28 0.28	
	(days) 654	Age productions (days) mon Sugar	

*Fruit only. †Fruit and stem.

	Table	6.	Starch	production	by	cassava.
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Crop age (months)	Starch production (tons ha ⁻¹ month ⁻¹		
10*	0.57		
12†	0.72		
15†	0.91		
21†	0.84		
Average	0.76		

*Data from experimental plots in Costa Rica (60). †Data from experimental plots in Jamaica (60). (10).

Table 7. Alcohol production and its relation to water use by sugarcane, pineapple, and cassava.

Crop	Ethanol production (liters ha ⁻¹ month ⁻¹)*	Water require- ment per month (mm) [†]	Water use effi- ciency (liters ethanol/ mm water)
Sugarcane	921	180	5.1
Pineapple	964	83	11.6
Cassava	611	125	4.9

Calculations are based on conversion of sugar or starch yield, or both, given in Tables 4-6, to ethanol. +Water requirement for optimum growth of sugar-cane is the mean of the range given in (12). For pincapple we selected 1000 mm per year as being representative of areas where good yields are obtained consistently (7); data for cassava are from

yield of approximately 5.5 calories per calorie of input prior to conversion to alcohol but no data are available on stem harvesting or processing costs. Processing costs for conversion of pineapple carbohydrates to alcohol presumably would be greater than for sugarcane but less than for cassava because the fruit sugars are readily fermentable. Both cassava and pineapple can be grown in infertile soils, but their water use efficiency (Table 7), especially in the case of pineapple, makes them particularly appropriate crops for many areas where water for irrigation is limited or nonexistent. There are approximately 170 million hectares of land in the Cerrado of Brazil alone which are not now being cultivated because total rainfall, its seasonal distribution, and soil fertility limit productivity of conventional crops. With good management practices, these areas probably could be profitably planted to cassava or pineapple, or both, for energy production.

One possible advantage of cane over the other crops is that cane distilleries are often self-sufficient in energy, generating heat and electricity by burning bagasse. It has been estimated that bagasse has an energy content of 1300 kilocalories per kilogram (49). Cassava and pineapple residues have too high a water content to burn, but it has been proposed that pineapple be sun-dried in the field for use as a source of combustibles (54), and cassava residues no doubt could be similarly utilized. The energy content of air-dried pineapple plant residue has been estimated to be 3300 kcal/kg (55). Cassava and pineapple leaf residues are good sources of roughage for cattle (1,53) so most of the energy stored by these two crops could also be recovered as livestock feed.

In Hawaii, 700 to 800 hectares of ratooned pineapple plants yielding 60 to 70 metric tons of fresh plant material per hectare are being harvested annually for cattle feed. Plants are cut 15 to 20 centimeters above the soil so most of the plant stem is chopped with the leaves. Separation of stems for fermentation would reduce the tonnage and energy content of the feed, but the leaves alone are a good source of roughage (56, 57). The pineapple stem also yields relatively large amounts of bromelin, a proteolytic enzyme having commercial value.

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Should There Be a Commission on Medical Education?

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I have been asked to address the question: Is there a need for a national commission to review medical education in the United States? In response, I propose to deal with the process of education for medicine that usually takes up the first 6 years: the premedical and preclinical phases. I do this for three rea-

undesirable features and manifest defects in the final product of the sytem, which is, of course, the licensable physician (1). The third reason is that I believe the clerkship method for teaching clinical medicine is, in principle, entirely correct and not in any way to be confused with the pre-Flexnerian apprenticeship system

Summary. In its premedical and preclinical phases our present scheme of education for medicine is intellectually deficient, wasteful of money and time, and in urgent need of overhaul. The author defines conditions under which a national commission might possibly set the educational process on the road to reform.

sons. The first is to reduce the topic to manageable size and, at the same time, to recognize that the premedical and preclinical sciences overlap and can be integrated to a far greater degree than is ordinarily permitted. The second is that for more than half a century the premedical and preclinical phases have been thought to be responsible for certain

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under which a medical student depended completely on the whims and expertise of a single practising physician for his clinical training. Very probably the curriculum of the future will emphasize clerkships in the basics, that is, medicine, surgery, psychiatry, pediatrics, and possibly obstetrics and gynecology. Clerkships in the various subspecialties

ought to be elective, or they ought to be firmly postponed to the post-M.D. period. But in essence, the clerkship method of clinical training, under ideal conditions, ought to bring to bear a sensible mix of the academic and the practical, as it already does in many institutions, and is per se a very heady intellectual and social experience. What the clerkship needs is not revision but polishing and perfecting.

It is quite otherwise with the first two phases of the process. One might add, in passing, that ideally the whole process ought to be a continuum; many medical educators maintain that it is precisely that. Yet the several faculties that are directly concerned routinely do everything they can to keep the process rigidly segmented. And thanks to that effort, among other things, education for medicine in its premedical and preclinical phases is intellectually deficient, horrendously wasteful in money and in time, and in urgent need of overhaul.

Another Flexner Campaign?

We often hear it said that what we need is another Flexner report, as if one could turn the clock back from the late 1970's to the first decade of the century. Actually Flexner's effort, gifted man though he undoubtedly was, was something of a fluke. He came on the scene

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